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ON FLUTING OF THE TRUNK IN YOUNG TREES OF *PINUS TAEDA* L. (LOBLOLLY PINE)

WITH AN APPENDIX ON THE MEASUREMENT OF RADIAL GROWTH AS RING-WIDTH

By I. V. Newman*

[*Manuscript received March* 18, 1955]

Summary

Appearance of fluting of the trunk in young trees of *Pinus taeda* L. (loblolly pine) from Queensland is due to near alignment of greatly extended depressions produced by suppression of radial growth above and below the insertion of branch-bases. Inclination of the fluting accompanies inclination of grain (spiral grain) in the tree.

This suppression, chiefly of early wood, operates for 2-3 years and differs from the very slightly extended suppression associated normally with *dead* branch-bases on both normal and abnormal trees. A pathological condition of the cambial zone seems to affect not only the quantity but also the structure of the cells formed.

In the two butt logs examined, suppression occurred only in the growing seasons beginning 1948, 1949, and sometimes 1950. After that, the depressions were being obliterated by local excess of radial growth, mainly in apparent late wood, and the surface would probably have appeared undisturbed by the end of the season beginning 1955 or 1956 (trees about 18-20 years old).

In a note on measurement of "radial growth" at a grooved surface, of the three possible measurements of *ring-width*, namely, *radial* (along the radius of the tree-as-a-whole), *histological* (along the direction of the rows of wood cells), and *apparent* (along the shortest distance across the ring), the histological ring-width is suggested as most correctly representing "radial growth". The implied "stepped" arrangement of the cambium is demonstrated.

I. Introduction

The appearance of spiral fluting in young trees (approaching 15 years old) of *Pinus taeda* L. (loblolly pine) has been observed in Queensland. About 5 per cent. of the progeny of one open-pollinated tree show this condition. The Queensland Department of Forestry submitted butt logs of two "fluted" trees and one "normal" tree for examination. A full solution of the cause of fluting would probably need continuous observations on the living trees. However, the anatomical details observed in these few specimens, and their implications, seemed worth putting on record.

One of the fluted logs (unknown parentage) was felled (March 1953) at Tibrogargan logging area, Glass House State Forest. The other fluted log (June 1953) and the normal log (mid August 1953), progeny of the one open-pollinated tree TS2, were felled at Beerwah State Forest. All three trees are regarded as having been felled essentially at the end of the growth season that began in 1952. Throughout this paper, the annual ring or growth season will be indicated by the year in which it begins, and so, *1952* (season or ring) *late wood* may be laid down actually in 1953.

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II. General Appearance of the Logs

The log from the normal tree had the usual superficial features and sectional appearance of *P. taeda* (Plate 3). The logs from the abnormal, "fluted", trees also had the usual surface texture of bark and wood; but the form of the surface showed extensive longitudinal grooves in which branch-bases were situated (Plate 1, Figs. 1(i), 1(ii), and 2-5). Because these grooves are due to suppression of radial growth, and not to any excess growth, the abnormal form of surface is described as "fluted", rather than as "ribbed" (Plate 2). Each branch-base lies in its own depression which, extending further below than above, may have a total length of over ½ m in the abnormal logs (Plate 1, Figs. 2-5). Where two or more depressions stand nearly in line, the long grooves of up to 1½ m produce the appearance of fluting which, in these logs, followed a spiral course. But all three logs, normal and abnormal, showed spiral grain with left-hand upward inclination as is common in the genus *Pinus* at a similar age. It is, then, reasonable to assume that the fluting merely takes the inclination of the contemporary grain.

Table 1

LENGTH OF DEPRESSION AND DIAMETER OF BRANCH WOOD

Branch-base	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Length of depression, *ld* (cm)	90	43	73	76	40	72	50	68	70	50?	0
Diameter of branch wood, *dbw* (mm)	21	24	18	23	10	11	10	13	11	26	4
Ratio— *ld*/*dbw*, whole numbers	43	18	41	33	40	66	50	52	64	19	0

Measurements of the lengths of the depressions (*ld*) and the diameters of the branch wood (*dbw*) on the specimens of the abnormal butt log shown in Plate 1, Figures 2-5, are set out in Table 1. These values and the ratio *ld*/*dbw* are plotted in Figure 1, in order of increasing size of the branch-bases which may be grouped in three approximate size ranges, namely, (XI), (V, VII, VI, IX, VIII), and (III, I, IV, II, X). That the curve for *ld*/*dbw* does not approximate to a straight line shows that extent of depression is not dependent on *size* of branch-base (e.g. as a quantitative source of toxin). Each of the two groups of five branch-bases roughly approximates to constant size. Within each group the curve for *ld*/*dbw* varies in the same sense as the curve for *ld*, which it should do were *dbw* constant and *ld* dependent on a factor unrelated to the *size* of the branch-base.* Thus it appears that the cause of the depressions on the abnormal trees, though sited in relation to the branch-bases, does not operate in relation to their size as such.

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* Juxtaposition of III and IV would make an exception. As their difference in length is only 3 cm in a total of approximately 75 cm, this does not destroy the overall picture; for the lengths of the depressions cannot be measured with precision.

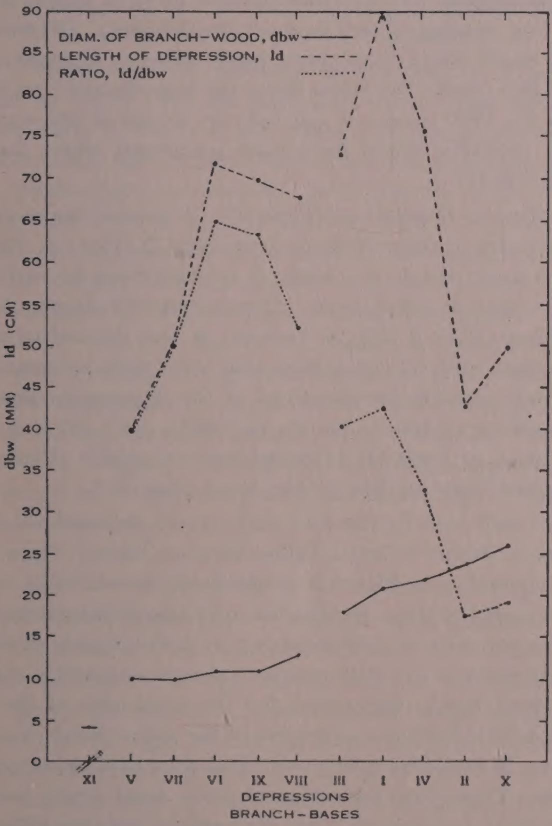

Fig. 1.—Abnormal tree. For explanation see text.

III. Structure of Butt Logs

(*a*) *Macroscopic Description of Abnormal Log*

Both abnormal logs show the same features. This description is based on polished* disks located as shown in Plate 1, Figure 1(ii) (continuous with Fig. 1(i)) and viewed as though looking down the trunk. Growth disturbance first appeared early in the 1948 season. Through the region of disturbance, ring structure, even false rings, can be traced. The greater tangential extent of the suppression in the later-formed (outer) parts of the disturbed area shows that the effect in the cambial zone spreads laterally with time (e.g. depressions *B* and *D* in Plate 2, Fig. 6). Radial delay of suppressive effects, as at *A′* in Plate 2, Figure 6, shows a vertical spread with time. The extension of the depressions further below than above the branch-bases (Plate 1, Figs. 2-5) hints at the phloem (inner bark) as the path of transmission, the cambial zone being the place of action.

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* Polished with successively finer grades of sandpaper, finished with ordinary brown paper.

The depressions appear to be either narrow (always single) or broad (often multiple, representing overlap of two or more depressions). Detailed examination, as outlined below, shows that: suppression varies across a depression and varies as between early and late woods, the latter being the less affected; recovery, beginning from some time in the 1950 season, is generally by excess of late wood; obliteration of the depressions probably would have been completed about 3 years after the time the tree was felled.

(i) *Details of Narrow Depressions* (Plate 2).—A minute depression, like others in this material, appears in the middle of depression *D* (Plate 2, Fig. 6) associated with the trace of a dwarf shoot or a scale; it is obliterated by early wood of 1948 season, though in a zone of suppression. Larger, but still simple, depressions, still obvious at the surface (Plate 2, Fig. 6, between *A* and *A′*, and in rib III), have a vertical extent of only about 1-2 cm, appear associated with previous small branches or dwarf shoots, and resemble accentuations of the depressions present sometimes on pines in the condition of timber known as "bird's eye". If long enough and in line, they may appear to form an extended narrow groove (Plate 1, Fig. 1(ii)). They are also inclined more or less as the local grain is.*

The details are well seen in the two very similar depressions in rib III, at a lower level on Plate 2, Figure 6, and a higher level on Plate 2, Figure 8 (cf. Plate 1, Fig. 1(ii)). The depression in Figure 8 is the more distant from its branch-base. The false rings are useful guides. Except for mechanical disturbance due to knots, radial growth shows normally at both levels up to the beginning of the 1948 season. It is clear that early wood of the 1948 season is almost completely suppressed in the first false ring at both levels, suppressed for the remainder of the season at the lower level, but with little further suppression at the higher level. Late wood of that season is, if anything, in excess at both levels. This pattern is approximately repeated in the 1949 season. Thereafter, formation of early wood seems normal in extent, whilst excess late wood is filling in both depressions towards obliteration by the end of the 1952 season. In thus judging amounts of wood formed, one should not confuse radial growth and apparent ring-width. (See Appendix I on the measurement of radial growth as ring-width.)

(ii) *Details of Broad Depressions* (Plate 2, Fig. 6).—Following the above description, one may easily discern the details of the broad, often complicated, depressions—multiple at *A*, *B*, and *D*; single at *C* and within rib II. The components of the multiple depression may be observable, as in *B* which is distant from the three originating branch-bases (Plate 1, Figs. 1(i) and 1(ii)); or the depression may be almost uniform, as in *D* which also has three originating branch-bases. The two sides may differ, with origins at different distances (*A* and *A′*). The depression in rib II, first marked by complete suppression of the first 1950 false ring early wood, probably began with the "flattening" of the 1949 false ring but was temporarily compensated by excess late wood that year. By similar means the 1950 suppression was almost compensated by the time of felling. The branch-base involved is either small and already engulfed at another level nearby, or is too distant to be seen on the portion of trunk represented.

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* Some observations of "bird's eye" on *Pinus radiata* suggest that the small depressions retain the inclination of the grain at their time of origin, though the grain inclination may change in the subsequently formed wood in which the depressions are maintained.

(iii) *Purple Deposit.*—In the disturbed regions there is a dark purple deposit, visually different in colour from the dark late wood. The orthochromatic plates used in preparing Plate 2, Figure 6, and Plate 3, Figure 11, do not record this difference. A panchromatic plate with a yellow filter, while photographically lightening the late wood, darkens the purple deposit, as in Plate 2, Figure 7 (*p*) and Figure 8. (Note its absence from Plate 3, Figs. 12 and 13.) Figure 7 compared with Figure 6 shows the heightened contrast of the deposit at the beginning of the depression in rib III, and its absence from the smaller depression between *A* and *A′* (which may point to a cause of the size difference of these depressions). In the higher level depressions in rib III (Plate 2, Fig. 8) the deposit is possibly at the very end of 1947 late wood and certainly at the 1948-9 ring junction. Such deposits, clearly to be seen in other depressions in the abnormal disks (Plate 2, Figs. 6 and 8) are quite absent from the normal disks (Plate 3, Figs. 11 and 12). This deposit, peculiar to the abnormal tree, suggests a metabolic disturbance associated with the suppression. Microscopic examination reveals it in regions where it is not dense enough to be seen with the naked eye.

(*b*) *Microscopic Study of the Disturbed Region*

The difference in suppression of early and late wood implies that the suppressive factor has a qualitative as well as a quantitative effect. Confirmed by microscopical examination, this is in harmony with the inference of metabolic disturbance from the presence of the purple deposit. Transverse and radial longitudinal sections of disturbed regions (Plate 4, Figs. 15 and 16) show clearly the presence of the purple deposit as a marginal band or a complete filling in some or all of the cells in a neighbourhood; they also show the distortion from the normal cell structure of pine wood as an increase in the number of ray tracheids tangentially and vertically and as a reticulate thickening of walls of both horizontal and vertical tracheids. Intense disturbance leads to cleavage between the normal core and the outer disturbed wood (*cl* in Plate 1, Fig. 1(iii)).

IV. Indications of the Cause of Fluting

It has been shown already that the fluted appearance is due to grooves formed by approximate alignments of extensive depressions related to the positions of branch-bases. Search for a cause involves a comparison of what occurs near branch-bases in the normal and abnormal trees. A vertically short depression appears in both, but in the abnormal tree it is overrun and obscured by the abnormal suppressive activity.

A branch-base engulfed by the expanding trunk will be referred to as a knot. The normal disks shown on Plate 3, Figures 12 and 13, show the following features: where the outer side of a knot lies within the general radial range of a ring, that ring suffers some general suppression in that region; if a subsequent ring is brought into a similar relationship to the knot by that suppression, it also suffers some suppression (e.g. at knot *D* in Plate 3, Figure 12, and the ring 1947 followed by the ring 1948 at knot *C* in Plate 3, Figure 13, and at knot *B* for the ring 1946 in Figure 13); if the inner edge of a knot lies within the normal radial range of a ring, there is a curious slight lateral suppression of the ring, a little displaced to either side of the knot (e.g. for knot *B* in the 1946 ring at the level shown in Plate 3, Figure 12, and in the 1945 ring at the level shown in Plate 3, Figure 13). These features can be seen also in the abnormal tree (Plate 2, Figs. 8-10): lateral small suppressions in the 1947 ring at knots *B* and *C* (Plate 2, Fig. 8, in the resinous area), and in the 1946, 1946, and 1945 rings at three levels of knot *A* (Plate 2, Figs. 8, 9, and 10 respectively); general suppression in knot *A* (Figs. 9 and 10), the only one with its outer edge in relation to normal wood.

Obviously, such features will be complicated by mechanical effects, if the branch-base which is becoming a knot is already dead at the time the expanding trunk reaches its inner or outer face. For, there will then be no cambial continuity to give tissue continuity between wood of trunk and of knot. Thus, the branch-bases at *A* and *C* in Plate 3, Figure 12, appear to have died when about half engulfed; internally there is full tissue continuity, but along the outer part of the knot there is none. The *branch-base* *C* of the abnormal tree (Plate 2, Fig. 8) is closely similar to the *knot* *C* in the normal tree; the centres of both are at the radial level of the late wood of ring 1947; but in the abnormal case engulfment has been delayed by the abnormal suppression that produces the long depressions (and so the structure is still a branch-base, not a knot).

A feature common to the two knots and the branch-base just mentioned is a dark resinous appearance occupying the inner segment of the structure, corresponding to the arc of tissue-continuity. The remaining (outer) segment, corresponding to the arc of tissue-discontinuity, does not show this appearance. Associated with the region of the branch-base engulfed while alive, this appearance is almost confined to the knot in the normal tree (Plate 3, Figs. 12 and 13), but in the abnormal tree extends into the trunk tissue—even to the pith at some levels, where the whole resembles the silhouette of a thin-stemmed goblet (Plate 2, Figs. 8-10). Longitudinally, the darkening extends downward more than upward, near the bark, and upward more than downward, near the pith (Plate 1, Fig. 1(iii)).

In relation, then, to the presence of branch-bases *as such*, neglecting the resinous appearance, the normal and abnormal trees show not the slightest significant difference, as shown by close comparison of abnormal knot *A* (three levels shown in Plate 2, Figs. 8-10) with normal knot *B* (two levels shown in Plate 3, Figs. 12 and 13).

Death of the branches (or branch-bases, if live-pruned) occurred in the abnormal tree from late in the 1947 season to late in the 1948 or perhaps the 1949 season; in the normal tree it seems to have been later, perhaps not till early in the 1950 season. These details have been worked out on the logs (normal and abnormal) from the Beerwah State Forest, where it is reported that no pruning was done till about 1951. The abnormal log from the Tibrogargan logging area, where pruning was first done in 1947, is essentially similar to the other one, with suppressive activity beginning in the 1948 season. It seems doubtful, therefore, whether pruning could be always related to the abnormal suppressive activity. Nor, by the timing, could death of the branch-base be related causally to it. In the higher regions of the abnormal butt logs, i.e. some 1-1½ m above the level described in detail, some suppressive activity possibly began at a later date.

V. CONCLUSION

In the abnormal trees examined, some disease factor (whether of internal physiological origin or of external infective origin is not clear) would seem to have spread from the branch-base, causing suppression of radial growth over an extensive vertical range for only some 2-3 years. It may or may not be related to the death of the branch, and may operate before that. Apparently a minority of trees is susceptible to this factor which might be operative at a particular age of the annual shoot. Recovery occurs, chiefly by excess formation of late wood; and probably 6 years later the trunk would show no sign of the fluted condition at that level. Higher up the tree, however, we could expect the process of fluting and recovery to occur at the times appropriate to the particular ages of the successive annual shoots. In support of this interpretation, a letter from the Queensland Department of Forestry referring to an older tree, planted in 1932 and pruned to a height of 21 ft, may be quoted: ". . . fluting is most prominent at the top of the pruned section and extends into the lower part of the crown. Fluting is not evident in the butt sector . . .". It could be expected that the butt sector would show the fluted state *internally*, unless, of course, the disturbing factor made its appearance in the locality only about 1948, and not earlier.

A practical conclusion could be that the fluted condition is due to a factor (possibly an infective factor) suppressing radial growth for a limited period of 2-3 years and beginning at approximately the same age of any annual shoot. Whether the fluting follows a spiral course depends on whether the grain was inclined at the time the suppressive factor was in operation, and will not be relevant to the problem of fluting. *Provided there is no subsequent appearance of the disturbing factor at that level*, the disturbance of structure will not extend beyond a diameter of about 15-17½ cm and would therefore make little difference to the commercial value of the tree for timber or peeling; it might even provide attractive figure.

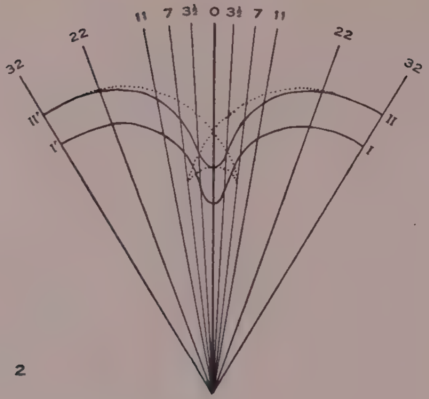
VI. ACKNOWLEDGMENTS

The author thanks Dr. H. E. Dadswell, Officer-in-Charge of the Section of Wood and Fibre Structure, for bringing the problem of fluting before him. To Mr. Albert L. Lee, the author is indebted for the photographs of logs and disks, and to Miss E. M. Valentine, for her help in preparing the material.

APPENDIX I

THE MEASUREMENT OF RADIAL GROWTH AS RING-WIDTH

Normally we expect to measure lateral increase ("radial growth") of a trunk or branch along the radius at the selected point, that is, orthogonally ("perpendicularly") to the surface of the organ concerned. For normally concentric growth,



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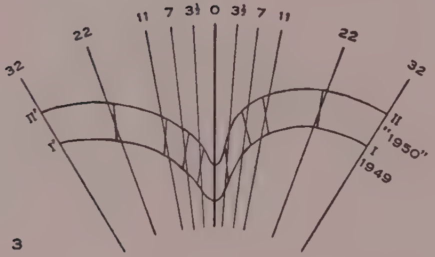

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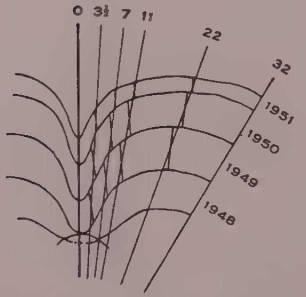

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Figs. 2-4.—Theoretical and actual representations (reduced) of ring-width at a depression in *Pinus taeda*. The line 0 represents the radius of the trunk-as-a-whole through the mid point of the depression; the lines 3½, 7, 11, 22, 32, represent radii at the named angles. A value of 11 mm for constant widths was chosen for the originals of Figures 2 and 3 as approximating to the histological width of the 1950 ring at depression B in the original photograph for Plate 3, Figure 12.

Fig. 2.—Theoretical diagram of constant "radial" and "apparent" ring-widths: I-I′ reproduces a tracing, and its mirror image, of the right half of the end of the 1949 ring at depression *B* in the original; the lines II-II′ represent the "rings" of constant "radial" width (continuous) and constant "apparent" width (dotted).

Fig. 3.—Theoretical construction of a ring of constant "histological" width: I-I′ is as for Figure 2, on the right, and, on the left represents some other form for comparison; II-II′ represents the end of a theoretical ring for "1950" of constant "histological" width.

Fig. 4.—Actual tracing from the original photograph of the 1948-51 rings, on the same scale as Figure 3: the directions of the tracheid rows across the rings are marked, except for the 1948 ring involved with a knot.

this geometrical idea gives a good measure of the anatomical occurrence—the activity of the cambium in adding to the thickness of the organ. In plant structural terms, we are measuring along the row the increase in length of rows of cells. But, in irregularly growing trunks, the direction of the rows is frequently not orthogonal to the surface of trunk or ring. This was very evident in the fluted specimens of *Pinus taeda* described in the present paper. At the sides of depressions (normal or abnormal), estimates of more or of less "radial" growth were made, *not* along the shortest distance across a ring, but along the tracheid rows, if discernible, other-

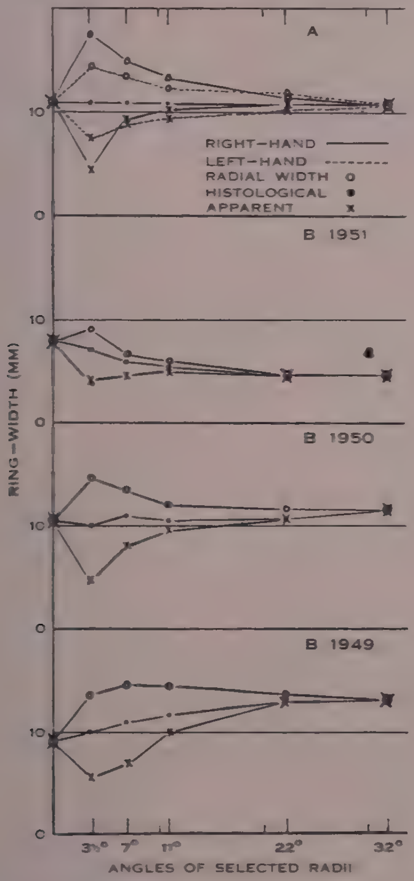


Fig. 5.—Graphs representing types of ring-width at a depression in *Pinus taeda*. The values plotted are based on measurements of the original photograph for Plate 3, Figure 12, depression *B*. For explanation, see text. *A*, theoretical, based on a constant histological width of 11 mm as in Figure 3; *B*, actual, based on measurements for the years 1949, 1950, and 1951, as in Figure 4.

wise along the radius of the trunk-as-a-whole. The following considerations support this practice.

The width of a ring at any point can be assessed in three ways: *radial width*—distance across the ring along the radius of the trunk-as-a-whole; *histological width*—distance across the ring along the tracheid or fibre rows; *apparent width*—shortest distance across the ring. In a perfectly regular trunk, all three will coincide.

Figure 2, on the basis of the end of the 1949 ring at depression *B* in Plate 3, Figure 12, shows that a ring of constant *radial* width "narrows" on either face of the depression, i.e. its *apparent* width shows two minima, and that a ring of constant *apparent* width, interesting as a geometrical figure, would be completely unreal as a plant structure. The radial width (continuous line II-II′) would the more nearly represent a growth situation. However, the ring shown in Figure 3 (on a similar basis to Figure 2, on its right side) is still more nearly actual, representing for the year "1950" a constant *histological* width, which is intermediate between radial and apparent widths. All three "widths" converge to equality at the central lines of the "groove" and of the "ribs" to either side. Graph *A* in Figure 5 sets out the curves (plotted against selected radial angles) for the three types of width as measured on the original for the printed diagrams. Note the two points of convergence mentioned above.

The actual forms of the limits of the rings 1948-1951 inclusive, at the right-hand side of depression *B* in Plate 3, Figure 12, are represented in Figure 4. The three graphs, *B* 1949, 1950, and 1951, in Figure 5, plotted as for graph *A*, present the curves for the rings of those three years. Compare them with the continuous line curves in graph *A*. In the original of Figure 3, the width 11 mm was chosen as approximating to a smoothing of the histological width of the actual 1950 ring. This figure and graph thus become *theoretical* representations for the *actual* ring 1950 of Figure 4 and graph *B* 1950 of Figure 5. For the three rings, the actual curves for histological width are adequately smooth, unpeaked and untroughed. They show cambial activity, constant throughout the depression for the 1950 ring, but increasingly suppressed for the 1949 ring and augmented for the 1951 ring, towards the centre of the depression.

This short note suggests that in all cases of measurement to express excentric growth of trees in terms of width of ring, it should be the *histological width* that is measured, not the *apparent width*. This implies that the cambium does not lie with its "tangential" walls always parallel with the surface of the wood, but may, in at least some cases of excentric growth such as described in the paper above, lie in stepwise fashion around the surface of the wood in a depression. Plate 4, Figures 17*A*-*C* show structure at a depression where this stepwise arrangement of the cambium had obviously occurred, and the "radial" rows are inclined to the ring-surface.

EXPLANATION OF PLATES 1-4

PLATE 1

Pinus taeda: Butt logs and disks from abnormal (fluted) trees. Reduced to (approx.): Figures 1(i) and 1(ii), 1/6; Figure 1(iii), 1/5; Figures 2-5, 1/10.

Fig. 1(i) and 1(ii).—Two consecutive parts of a fluted log, viewed from slightly different angles. Capital letters mark the depressions as on Plate 2. Roman numerals similarly mark the intervening ribs. The single and double primes indicate that the depressions and ribs concerned may be in relation to different branch-bases from those relevant to the illustrated disk surfaces; *b*, *b′*, and *b″* indicate the branch-bases (or the levels of them) originating the components of the multiple depression *B*. Figure 1(i) shows the normal bark, the whorl near the base, and the inclination of the depressions. Figure 1(ii) shows the part cut into disks at the five levels marked at the extreme left of the figure. The numbers at the left are the numbers of the plate figures representing the levels indicated by the arrows. Part of the bark has been removed, showing in rib III abnormal extension of small depressions such as may, in normal extent, produce "bird's eye" in timbers.

Fig. 1(iii).—Shows the label-bearing disk in Figure 1(ii) split along the diameter *BD* of Figure 8 on Plate 2, *B* being to the left, *D* to the right, and *C* behind. The resinous stain shows darkly in association with the knots (branch bases). *cl* shows the position of two cleavage lines where suppressive and distorting activity was extreme.

Figs. 2-5.—Surface view of the four quarters of an abnormal log (cut into three for convenience of photography). Roman numerals to the left are at the levels of branch-bases. The extent of the depressions is indicated by white lines, and branch-bases not obvious by white crosses. Note the inclination of the depressions and their near alignment to form long grooves, e.g. I, VI, and X.

PLATE 2

Pinus taeda: Disks from abnormal butt log, viewed as though looking down; reduced to 3/5. For location, see Plate 1, Figure 1(ii), and its explanation. *AD* are depressions; I-IV, the intervening ribs. On Figure 6, *X* and *Y* are the radial locations of Figures 15*A*, *B* and 16*A*, *B* respectively on Plate 4; *Z* shows the location of Figures 17*A*, *B*, *C* on Plate 4. *p* indicates some examples of the purple deposit. Years of the beginning of annual rings are shown on Figures 6 and 8. For detailed explanation see text.

Figs. 6 and 7.—One and the same disk, away from a node. Figure 6 photographed on commercial orthochromatic plate *without* filter; Figure 7 on process panchromatic plate *with* filter (yellow), giving reduced contrast of late wood and increased contrast of purple deposit (*p*). (Photographs taken at different times; note difference in checking.)

Figs. 8-10.—Successively lower levels at a node, over a vertical range of about 1¼ cm, with 10 the closer to 9. Photography as for Figure 7. The small depression in rib III is not the same as that on Figures 6 and 7.

PLATE 3

Pinus taeda: Disks (wood only) from a normal butt log, near and at a node. Capital letters locate corresponding depressions.

Figs. 11-13.—As though looking down; reduced to 3/5. Above the node and at two successively lower levels at a node. For location, see Figure 14. Photography for Figure 11 as for Plate 2, Figure 6; for Figures 12, 13 as for Plate 2, Figure 7. Note that the disk shown in Figure 13 had acquired much blue-stain, which, with the yellow filter, shows up as short, dark, radial streaks, and emphasizes the resin canals. Years are shown on Figures 12 and 13.

Fig. 14.—Lateral view of two "contiguous" disks of a normal tree, showing normal short depressions associated with branch-bases. Reduced to ¼ (approx.). The disks appear separated because material was lost in squaring them off. Figures 11, 12, and 13 show respectively the upper and lower surfaces of the top disk and the upper surface of the bottom disk.

Plate 4

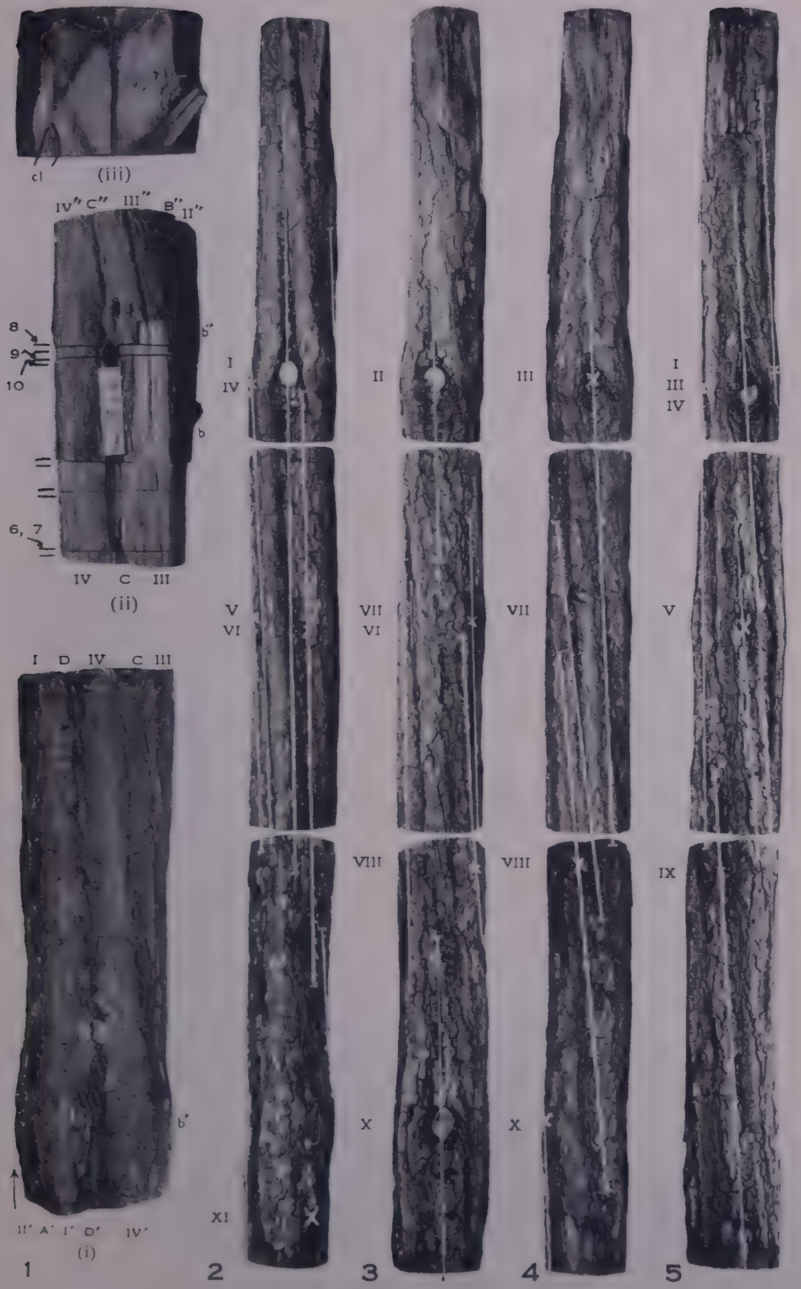
Pinus taeda: Photomicrographs of wood in abnormal butt log. Figures 15*A*, 16*A*, and 17*A*-*C* × 56; Figures 15*B* and 16*B* × 205. For locations see *X*, *Y*, and *Z* on Plate2, Figure 6; but the sections are taken at a little distance from the level of that disk surface.

Figs. 15*A* and 15*B*.—Transsectional views of abnormal wood, *B* being the area outlined in *A*. The disturbed region, in the neighbourhood of a false ring, shows no purple deposit (1948 season), but the first early wood of 1949 season (not included) has much deposit. Abnormal rays, several cells wide with reticulate tracheids, are present; also isolated groups of reticulate tracheids.

Figs. 16*A* and 16*B*.—Radial longisectional views of abnormal wood, *B* being the area outlined in *A*. The narrow tracheids at the bottom of Figure *A* end the 1948 late wood, the prominent disturbance being in 1949 early wood, including a false ring. Vertical, reticulate tracheids and increased number of ray cells are evident, with distortion of form. Purple deposit shows darkly in many cells as a peripheral band with "external knobs" filling the pits in the reticulate walls (knobs clear only in *B*).

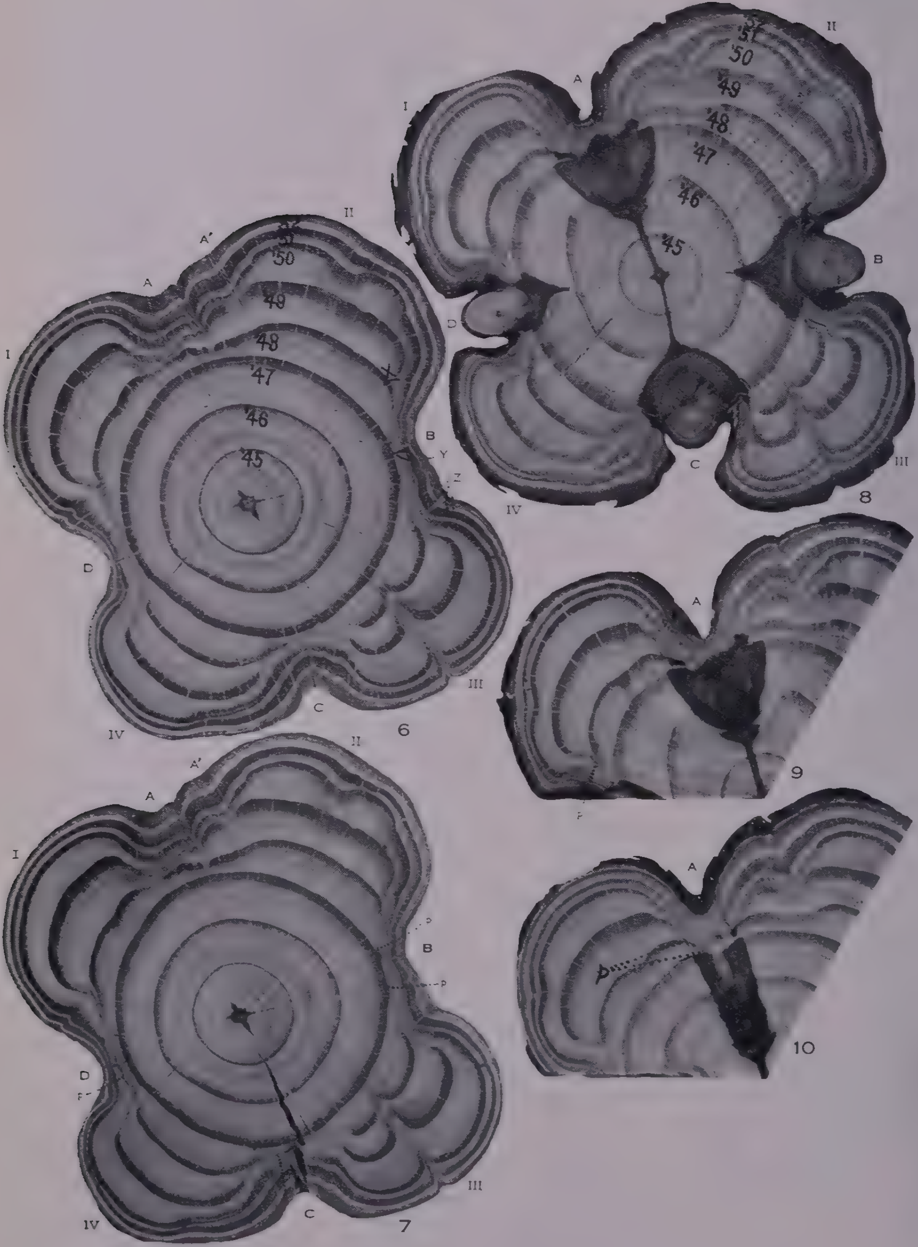
Figs. 17*A*-C.—Transsectional views of normal wood at a depression in an abnormal stem, but applicable for any normally depressed region as referred to in relation to text Figures 2-5. These photomicrographs show the result of stepwise arrangement of the cambium at the side (or any sloping face) of a groove. The radius of the trunk-as-a-whole through the mid line of the depression lies vertically along the page. The three figures, left to right, lie under the last dots of the guide-lines *Z*, top to bottom, in depression *B* in Plate 2, Figure 6. *A* and *B* are at the outer face of the 1951 wood and *C* at a double false ring in 1952 early wood. The tracheid rows are at an angle to the ring face (cambial tangent), with a slight tendency towards the perpendicular in the last late wood and first early wood.

FLUTED TRUNK OF PINUS TAEDA



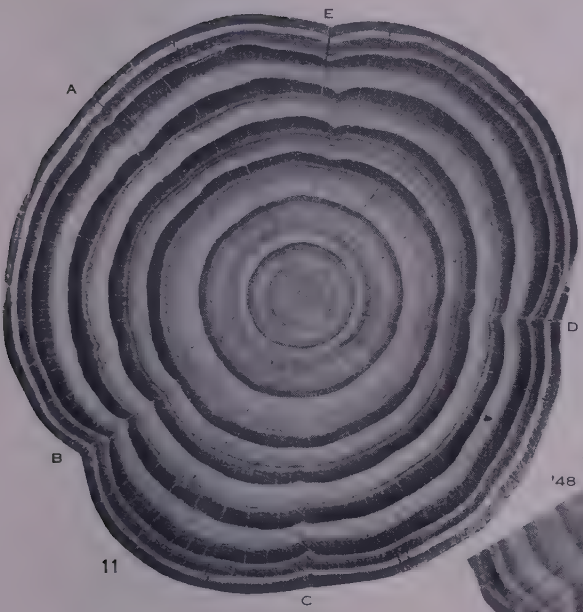
ABNORMAL LOGS

FLUTED TRUNK OF PINUS TAEDA

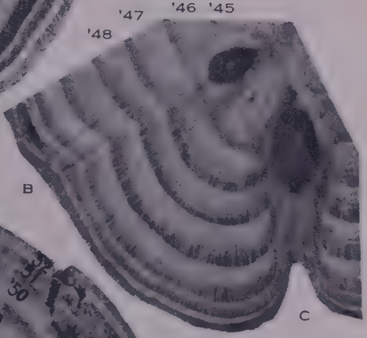


ABNORMAL INTERNODE AND NODE

FLUTED TRUNK OF PINUS TAEDA



11



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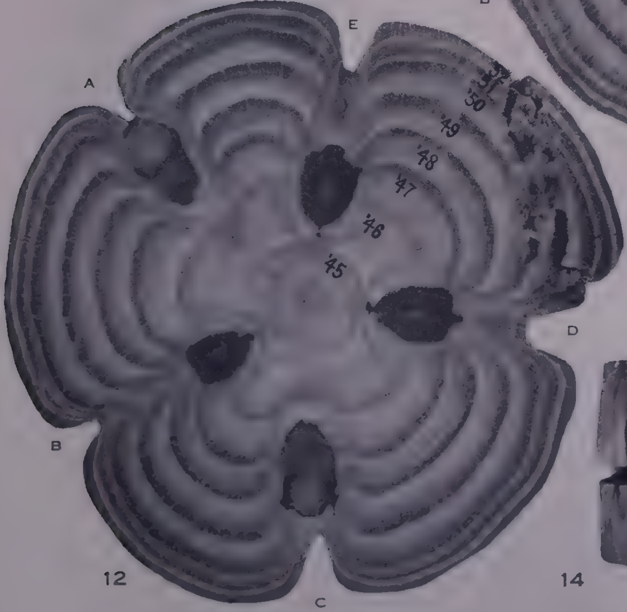
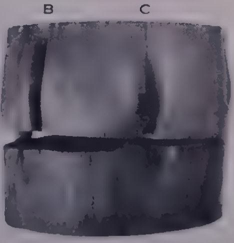


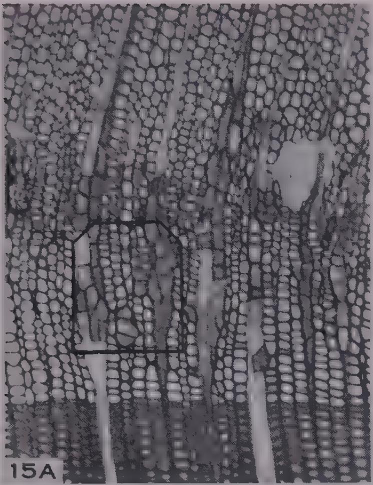
12

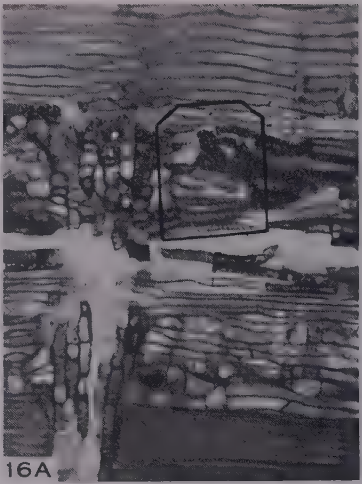


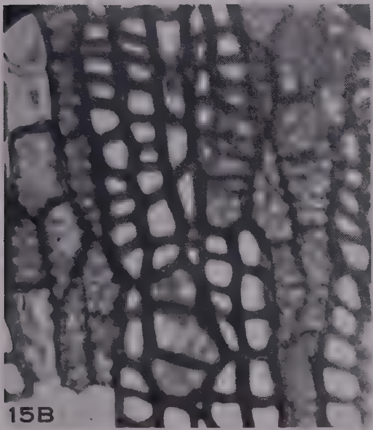
14

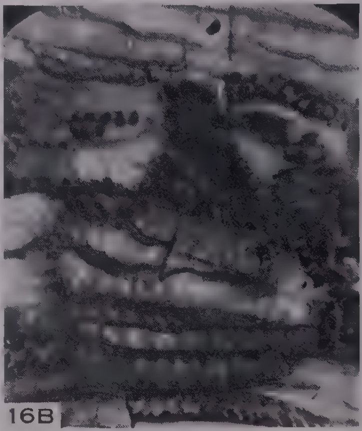
NORMAL INTERNODE AND NODE

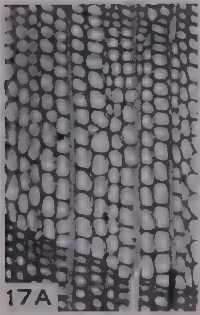
FLUTED TRUNK OF PINUS TAEDA

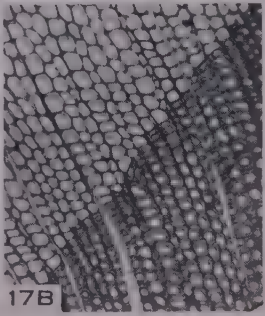

15A

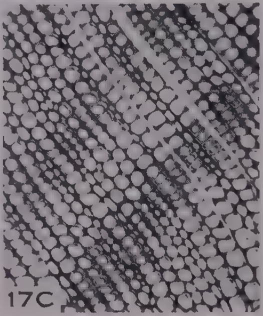

16A


15B


16B


17A


17B


17C

POLLEN MORPHOLOGY OF MYRTACEAE FROM THE SOUTH-WEST PACIFIC AREA

By KATHLEEN M. PIKE*

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Summary

The pollen grains of 300 species of 71 genera of the family Myrtaceae have been examined and their characteristic features summarized in tabular form.

The investigation has been mainly concerned with those species that occur in the south-west Pacific area, particularly Australia. For comparative purposes, the pollen morphology of a limited number of South American and two South African species has been included.

The significance of pollen characters for distinguishing genera and species within the family is discussed. In some instances pollen morphology has provided additional evidence for the classification of certain species as suggested by taxonomists.

A provisional key to pollen grains of the genera examined has been included.

I. INTRODUCTION

During palynological investigations of Cainozoic deposits in the Australian region, a number of fossil pollen grains was observed that resembled those of living species of the family Myrtaceae. In order to identify them it seemed desirable that the pollen grains of a large number of living genera within the family should be examined. The present account is the result of that study and, therefore, concerns mainly those species that occur in the Australasian region.

The botanical classification of the Myrtaceae by Niedenzu (Engler and Prantl 1893), with recent modifications and additions as shown by Ingle and Dadswell (1953), has been followed.

The Australian region is one of the two main areas of development of the Myrtaceae, and this family forms an important component of the present Australian flora. All the genera of the dry-fruited Leptospermoideae, with the exception of *Tepualia* Griseb. (a monotypic genus in Chile) are restricted to the south-west Pacific area. It has been possible to obtain pollen samples of all these, except the recently described genera *Whiteodendron* Steen., *Basisperma* C. T. White, and *Kjellbergiodendron* Burret. The majority of the succulent-fruited Myrtoideae occur in central and south America, and, although representatives of each tribe of this group have been studied, some of the South American genera have not been included in the present investigation.

The measurements and other pollen characters of the species investigated, except those of *Eucalyptus* which are treated separately in Table 2, are summarized in Table 1. The genera and species are arranged in alphabetical order to facilitate use of the table. Each generic name is succeeded by a number that indicates the tribe or subtribe to which it belongs. Niedenzu's tribes, numbered from 1 to 11, are considered in that order in the text.

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Table 1

POLLEN MORPHOLOGY OF MYRTACEOUS SPECIES STUDIED

The numbers succeeding each generic name refer to the tribes as numbered in the text.

A.A. = Arnold Arboretum, Massachusetts, U.S.A.; B.M. = British Museum (Natural History), London; brevi. = brevicolpate; Cc. = concave; Cv. = convex; F = pattern present but exceedingly faint; K. = Royal Botanic Gardens, Kew, England; longi. = longicolpate; M.H. = National Herbarium, Melbourne, Australia; M.U.H. = Botany School Herbarium, University of Melbourne, Australia; O = oblate; OS = oblate-spheroidal; para. = parasyncolpate; PO = peroblate; PS = prolate-spheroidal; Q.H. = Botanic Museum and Herbarium, Brisbane, Australia; S = straight; S.H. = National Herbarium, Sydney, Australia; SO = suboblate; SP = subprolate; syn. = syncolpate.

Material Examined		Pollen Morphology							
Genus and Species	Source of Material	Polar Dia. (μ)		Equatorial Dia. (μ)		Shape		Colpi	Pattern
		Range	Average	Range	Average	Sides of Amb	Class		
Acca Berg. (1)									
A. sellowiana (Berg.) Burret. Fig. 1	Cult. Melbourne, Vic.	9–14	12	18–21	20	S Cv.	O	para.	+
Acmena DC. (4)									
A. acuminatissima (Bl.) Merr. & Perry	Clemens 29942. Borneo ex A.A.	10–13	11	18–20	19	S Cv.	O	syn.	—
A. caudata Merr. & Perry	Endert 4451 ex A.A.	10–11	11	16–20	18	S Cv.	O	syn.	—
A. divaricata Merr. & Perry	Daintree River. Coll. Kajewski ex Q.H.	—	—	14–18	17	S Cv.	O	syn.	—
A. hemilampra (F. Muell. ex F. M. Bail.) Merr. & Perry	Locality unknown ex S.H.	11–14	12	14–17	16	S Cv.	SO	syn.	—
A. laevifolia (Ridl.) Merr. & Perry	Brass & Versteigh 1131 ex A.A.	9–12	10	14–16	15	S Cv.	O	syn.	—
A. macrocarpa C. T. White. Fig. 36	N.Q.N.C. 4986. Type. ex Q.H.	16–18	17	22–25	24	S Cv.	O	syn.	—
A. smithii (Poir.) Merr. & Perry. Fig. 35	Milton, N.S.W. ex S.H.	10–14	12	16–18	17	S Cv.	O	syn.	—
,, ,,	Maitland, N.S.W. ex M.U.H.	14–15	15	18–20	19	S Cv.	O	syn.	—
Actinodium Schau. ex Schlect. (11)									
A. cunninghamii Schau. Fig. 93. Plate 1, Figs. 8-10	Albany, W.A. ex M.H.	16–18	17	14–17	15	S Cv.	PS	—	—

AGONIS DC. (8)									
A. juniperina Schau.	King George Sound, W.A. ex S.H.	8– 9	8	8–11	9	Cc.	OS	syn.	—
A. linearifolia (DC.) Schau.	Forrest Field, Perth, W.A. ex S.H.	7– 9	8	9–11	10	Cc.	SO	syn.	—
A. marginata (Labill.) Schau. Fig. 63	Albany, W.A. ex M.U.H.	8–11	10	11–15	14	Cc.	SO	syn.	—
A. parviceps Schau.	Albany, W.A. ex M.U.H.	9–11	9	12–16	14	Cc.	O	syn.	—
ANGOPHORA Cav. (7)									
A. cordifolia Cav. Fig. 54	Kogarah Dist., N.S.W. ex S.H.	18–23	19	25–32	28	S	O	syn.; para.	—
,, ,,	Locality unknown ex M.H.	23–27	25	27–32	30	S	O	syn.; para.	—
A. costata (Gaertn.) Britt. Fig. 55	Johns River, N.S.W. ex S.H.	18–19	18	25–27	26	S	O	syn.; para.	F
A. floribunda Sweet.	Mallacoota Inlet, Vic. ex M.H.	13–27	21	31–36	34	S	O	syn.; para.	F
A. intermedia DC.	Belltrees, N.S.W. ex S.H.	14–18	15	23–29	26	S	O	syn.	F
A. lanceolata Cav.	Locality unknown. ex M.H.	17–25	20	28–36	33	S	O	para.	—
A. subvelutina Cav.	Nepean, N.S.W. ex S.H.	14–17	16	25–30	27	S	O	syn.; para.	F̄
,, ,,	Locality unknown ex M.H.	20–25	23	27–32	29	S	O	syn.	F̄
ASTARTEA DC. (10)									
A. ambigua F. Muell.	Phillips River, W.A. ex M.H.	9–10	9	13–15	14	S	O	syn.	F
A. fascicularis Labill. Fig. 81	Mt. Barker, W.A. ex M.H.	10–13	10	14–16	11	Cc.	SO	syn.	F
,, ,,	Swan River, W.A. ex M.H.	9–11	10	11–14	12	Cc.	SP	syn.	F
A. scoparia Schau.	Locality unknown ex M.U.H.	11–13	12	9–12	10	Cc.	OS	syn.	F
AUSTROMYRTUS (Ndz.) Burret (2)									
A. acmenioides (F. Muell.) Burret. Fig. 6	Acacia Ck., N.S.W. ex S.H.	7– 9	8	19–22	20	S Cv.	PO	longi.	+
,, ,,	Burringbar, N.S.W. ex S.H.	7–11	9	14–20	18	S Cv.	PO	longi.	+
A. bidwillii (Benth.) Burret	Macleay River, N.S.W. ex S.H.	6– 8	7	11–16	14	S	PO	longi.	+
A. fragrantissima (F. Muell. ex Benth.) Burret	Richmond River, N.S.W. ex S.H.	6– 9	8	11–16	14	S	PO	longi.	+

Table 1 (*Continued*)

Material Examined		Pollen Morphology							
Genus and Species	Source of Material	Polar Dia. (μ)		Equatorial Dia. (μ)		Shape		Colpi	Pattern
		Range	Average	Range	Average	Sides of Amb	Class		
Austromyrtus (*Continued*)									
A. hillii (Benth.) Burret	Pine River, Qld. ex S.H.	7– 9	8	13–16	14	S	PO	longi.	+
A. inophloia (Bail. & C. T. White) Burret	Coll. F. M. Bailey 1891 ex S.H.	7– 8	7	14–18	16	S Cv.	PO	longi.	+
A. racemulosa Burret. Fig. 8	Port Denison, Qld. ex S.H.	7– 8	7	14–16	15	S	PO	longi.	+
?*A. stricta* (Panch. ex Brongn. & Gris.) Burret. Fig. 9	Franc No. 1784, New Caledonia ex K.	9–10	9	14–18	16	S	O	longi.	+
A. tenuifolia (Sm.) Burret. Fig. 7	Richmond River, N.S.W. ex S.H.	5– 9	7	14–19	17	S	PO	longi.	+
Backhousia Hook. & Harv. (5)									
B. angustifolia F. Muell.	Locality not specified ex M.H.	9–11	10	13–14	14	S	O	syn.	—
B. bancroftii Bail. & F. Muell.	Locality not specified ex M.H.	9–11	10	15–20	19	S	O	syn.; para.	F
B. citriodora F. Muell. Fig. 38	Locality not specified ex M.H.	9–10	9	18–20	19	S	PO	syn.; para.	F
B. myrtifolia Hook. & Harv.	Near Audley, Nat. Park, N.S.W. ex S.H.	9–11	10	18–20	19	S	O	syn.; para.	—
Baeckea L. (10)									
B. behrii F. Muell.	Little Desert, Vic. ex M.U.H.	7– 9	8	11–14	12	Cc. S	O	syn.	—
B. camphorata R.Br. Fig. 79	Glass House Mts., Qld. ex S.H.	6– 8	7	9–11	10	S	O	syn.	—
B. gunniana Schau.	Mt. Barrow, Tas. ex M.U.H.	6– 9	8	10–13	12	Cc. S	O	syn.	—
B. leptocaulis Hook. f.	Mdm. Howards Plains, Tas. ex S.H.	8– 9	9	10–12	11	S	O	syn.	—
B. ramossissima A. Cunn.	Cult. Bot. Gardens, Melbourne	6– 8	7	11–14	12	S	O	syn.	—
B. stenophylla F. Muell.	Coff's Harbour, N.S.W. ex M.U.H.	7– 9	8	9–14	10	S	SO	syn.	—

BALAUSTION Hook. (10)									
B. pulcherrimum Hook. Fig. 78	Coll. Hamilton, W.A. ex S.H.	18–22	20	18–20	19	Cc.	OS	syn.	F
,, ,,	Yerbillon, W.A. ex M.H.	22–25	24	22–25	23	Cc.	OS	syn.	F
BEAUFORTIA R. Br. (9)									
B. anisandra Schau.	Kalgan Plains, W.A. ex S.H.	7–10	9	18–23	19	S	PO	para.	F
B. decussata R. Br. Plate 1, Fig. 5	Stirling Range, W.A. ex M.H.	16–20	18	26–29	27	Cc. S	O	syn.; para.	F
B. heterophylla (Turcz.) Domin. Fig. 76	Stirling Range, W.A. ex M.H.	12–13	13	25–27	26	Cc.	PO	para.	F
B. sparsa R. Br.	King George Sound, W.A. ex M.H.	16–20	18	19–25	23	Cc.	SO	para.	F
B. squarrosa Schau. Fig. 77	Cannington, W.A. ex S.H.	13–14	14	23–25	24	Cc.	O	syn.	F
CALLISTEMON R. Br. (8)									
C. lanceolatus Sweet.	Cult. Melbourne, Vic.	9–12	11	16–20	19	S	O	para.	F
C. salignus (Sm.) DC. Fig. 65	Bulladelah, N.S.W. ex M.U.H.	9–11	10	14–16	15	S	O	para.	F
C. viridiflorus DC.	Tasmania ex M.U.H.	9–11	10	15–18	16	Cc. S	O	para.	F
CALOTHAMNUS Labill. (9)									
C. chrysantherus F. Muell.	Kennedy Range, W.A. Coll C. Teichert 1949	11–14	12	16–20	18	S	O	syn.	—
C. gracilis R. Br.	Esperence, W.A. ex M.H.	12–15	13	16–20	18	Cc. S	O	syn.	F
C. quadrifidus R. Br.	Cult. Botanic Gardens, Melbourne	14–16	15	18–19	18	Cc. S	SO	syn.	—
C. sanguineus Labill.	Coll. Drummond 1854 W.A. ex S.H.	11–13	12	16–18	17	Cc. S	O	syn.	F
C. torulosus Schau. Fig. 70	Serpentine, W.A. 1901 ex S.H.	10–11	11	14–16	15	S Cv.	O	syn.	F
CALYCOLPUS Berg. (2)									
C. glaber (Benth.) Berg. Fig. 4	Trinidad Herb. No. 12505 ex K.	13–15	14	20–22	21	S Cv.	O	longi.	+
CALYPTRANTHES Swarz. (3)									
C. fasciculata Berg.	Trinidad Herb. No. 14484 ex K.	11–14	13	20–25	22	S Cv.	O	longi.	+
C. lucida Mart. Fig. 22	Macguire No. 24491 ex K.	11–15	13	18–25	22	S Cv.	O	longi.	+
CALYTHRIX Labill. (11)									
C. aurea Lindl. Fig. 84	Locality not specified ex M.H.	8– 9	9	11–14	12	Cc.	O	brevi.	—
C. gracilis Benth.	Coll. S. L. Duigan. W.A. 1949	12–15	14	14–20	16	Cc. S	SO	brevi.	—
C. tetragona Labill. Fig. 85	Warialda, N.S.W. ex M.U.H.	9–12	11	11–16	14	Cc. S	SO	brevi.	—

TABLE 1 (*Continued*)

Material Examined		Pollen Morphology							
Genus and Species	Source of Material	Polar Dia. (μ)		Equatorial Dia. (μ)		Shape		Colpi	Pattern
		Range	Average	Range	Average	Sides of Amb	Class		
CHAMAELAUCIUM Desf. (11)									
C. axillaris F. Muell.	Cult. Botanic Gardens, Melbourne	13–16	14	20–23	22	Cc. S	O	brevi.	–
C. uncinatum Schau. Fig. 91	Cult. Botanic Gardens, Melbourne	14–17	16	21–27	24	Cc. S	O	brevi.	–
CHORICARPIA Domin (6)									
C. leptopetala (F. Muell.) Domin. Fig. 50	Eastern Dorrigo, N.S.W. ex S.H.	6–11	7	16–18	17	S	O	para.	F
CLEISTOCALYX Bl. (incl. *Acicalyptus* A. Gray) (4)									
C. arcuatinervis Merr. & Perry	M.D. Sulit 8373 ex A.A.	7–9	9	11–14	12	Cc. S	O	para.	F
C. brongnartii Merr. & Perry	Wagape, New Caledonia ex S.H. 23533	7–9	8	12–15	14	Cc. S	O	para.	F
C. eugenioides Merr. & Perry	Seeman 156 ex A.A.	7–8	7	11–14	12	S	O	para.	F
C. gustavioides (F. M. Bail.) Merr. & Perry	Daintree River, Qld. Kajewski 1398 ex Q.H.	22–29	25	28–31	29	S Cv.	SO	para.	
C. longiflorus (A. C. Smith) Merr. & Perry	Storck. ex A.A.	6–7	6	10–14	11	S	O	para.	F
C. myrtoides (A. Gray) Merr. & Perry	Fiji. A. C. Smith No. 241. 1933 ex K.	7–9	7	10–11	11	S	O	para.	–
C. operculatus (Roxb.) Merr. & Perry	Port Darwin ex M.H.	6–7	7	11–15	12	S	O	para.	–
C. retinervis Merr. & Perry	Clemens 3777 ex A.A.	7–10	8	13–15	14	S	O	para.	F
C. seemannii (A. Gray) Merr. & Perry. Fig. 32	Fiji. Yeoward 47. Coll. 1894 ex K.	7–10	9	12–14	13	S	O	para.	F

CLOEZIA Brongn. & Gris. (6)									
C. angustifolia Bak. f.	New Caledonia ex Q.H.	9–10	9	13–14	13	Co. 8	O	syn.	—
C. buxifolia Brongn. & Gris. Fig. 44	New Caledonia. Prony 1914 ex M.H.	6–9	7	13–18	16	8	PO	syn.	—
CONOTHAMNUS Lindl. (8)									
C. trinervis Lindl. Fig. 69	Kalamunda. W.A. ex M.H.	9–12	10	22–27	25	8	PO	syn.	|
DARWINIA Rudge (11)									
D. citriodora Benth.	W.A. ex M.U.H.	18–20	19	23–29	26	Co.	O	brevi.	—
D. diosmoides Benth. Fig. 95	Israelite Bay, W.A. ex S.H.	9–11	10	18–21	19	Co.	O	brevi.	—
D. micropetala Benth. Plate 1, Fig. 7	Little Desert, Vic. ex M.U.H.	11–14	13	18–20	19	Co.	O	brevi.	—
D. pauciflora Benth. Fig. 94	Mingenew, W.A. ex S.H.	14–18	16	24–29	27	Co.	O	brevi.	—
D. vestita Benth.	Serpentine, W.A. ex M.U.H.	11–14	12	16–20	18	Co.	O	brevi.	—
DECASPERMUM Forst. (2)									
D. blancoi Vid.	Luzon, Philippines ex S.H. No. 18808	12–14	13	18–20	18	8	O	longi.	|
D. gracilentum (Hance) Merr. & Perry	Locality not specified ex A.A.	9–11	10	20–25	22	8	PO	longi.	|
D. hainanense (Merr.) Merr. Fig. 14	Locality not specified ex A.A.	9–13	11	23–27	26	8	PO	longi.	|
D. paniculatum (Lindl.) Kurz	Logan River, Qld. ex M.H.	6–7	7	12–17	16	8	PO	longi.	|
EREMAEA Lindl. (9)									
E. acutifolia F. Muell.	Locality not specified ex M.H.	13–14	14	20–23	22	8	O	syn.	F
E. beaufortioides Benth.	Coll. Steedman 1940 ex S.H.	7–11	10	20–23	22	8	PO	syn.	F
" "	Locality not specified ex M.H.	11–16	14	21–25	23	8	PO	syn.	F
E. ebracteata F. Muell. Fig. 71	Drummond. Coll. 1854, W.A. ex S.H.	9–11	10	22–26	23	8	PO	syn.	F
E. fimbriata Lindl.	W.A. Coll. 1948 ex S.H.	9–11	10	20–25	23	8	PO	syn.	F
E. pilosa Lindl	Tammin, W.A. ex M.H.	8–11	9	20–25	22	8	PO	syn	F
EUCALYPTUS L'Herit. (7) *see* Table 2									
EUCALYPTOPSIS C. T. White (6)									
E. papuana C. T. White Fig. 51	N.G.F. 2110. Milne Bay, Papua ex J.S. Womersley	9–10	9	13–15	14	8	O	para.	—

TABLE 1 (*Continued*)

Material Examined		Pollen Morphology							
Genus and Species	Source of Material	Polar Dia. (μ)		Equatorial Dia. (μ)		Shape		Colpi	Pattern
		Range	Average	Range	Average	Sides of Amb	Class		
EUGENIA L. (4)									
EUGENIA A									
E. albanensis Sond. Fig. 24	Durban, Natal. J. Medley Wood. No. 7668 ex S.H.	10–12	11	18–24	22	Cv.	O	longi.	+
E. capensis Harv. Fig. 25	Durban, Natal. J. Medley Wood. No. 6268 ex S.H.	11–15	14	18–23	21	S	O	longi.	+
E. macrohila C. T. White & Francis. Fig. 26	Kelsey Ck. Proserpine ex Q.H.	10–12	11	14–16	15	S Cv.	SO	?	+
EUGENIA B									
E. angophoroides F. Muell.	Meston's 1904 Exped. ex Q.H.	7– 8	7	11–14	13	S Cv.	O	para.	F
E. coolminiata C. Moore	Cult. Sydney ex S.H.	7– 9	8	13–15	14	Cc. S	O	para.	−
,, ,,	Cult. Sydney ex M.U.H.	8–11	9	11–14	14	Cc. S	O	para.	−
E. crebrinervis C. T. White	Alstonville, N.S.W. ex S.H.	5– 7	6	10–11	11	Cc. S	O	syn.; para.	−
E. cyanocarpa F. Muell.	Bulladelah, N.S.W. ex M.U.H.	12–16	14	16–20	17	S	O	syn.; para.	−
E. hodgekinsoniae F. Muell. Fig. 29	Locality not specified ex S.H.	9–11	11	14–16	15	Cc. S	SO	para.	−
E. luehmanni F. Muell.	Cult. Bot Gardens, Sydney ex M.U.H.	7–11	7	13–17	15	S Cv.	PO	para.	F
E. moorei F. Muell.	Near Mullumbunby, N.S.W. ex S.H.	6– 7	7	11–14	12	S	O	para.	−
FENZLIA Endl. (2)									
F. obtusa Endl.	Queensland ex M.H.	17–20	18	22–25	24	S	O	longi.	+
F. retusa Endl. Fig. 16	Gulf of Carpentaria ex M.H.	17–20	18	22–29	26	S	O	longi.	+

HOMALOCALYX F. Muell. (11)								
H. ericaeus F. Muell. Fig. 86	Nth. coast of Aust. Coll. R. Brown ex M.H.	11–14	13	20–25	22	S	O	syn.	+
H. polyandrus F. Muell. ex Benth.	Leichhardt Coll. ex M.H.	11–14	13	20–25	22	S	O	syn.	+
HOMORANTHUS A. Cunn. ex Schau. (11)									
H. darwinioides (Maid. & Betche) Cheel	Merriwa, N.S.W. ex S.H.	11–15	13	16–25	22	Cc. S	O	brevi.	F
H. flavescens (Schau.) A. Cunn.	Pilligar Scrub, N.S.W. ex S.H.	11–14	13	20–24	21	Cc. S	O	brevi.	–
H. wilhelmii (F. Muell.) Cheel. Fig. 96	Ely, N.S.W. ex S.H.	9–11	10	14–17	15	S	O	brevi.	–
H. virgatus A. Cunn.	Cape Byron, N.S.W. ex M.H.	—	—	18–20	19	S	O	brevi.	–
HYPOCALYMMA Endl. (10)									
H. angustifolium Schau.	Nedlands, W.A. ex M.U.H.	5– 9	6	14–17	15	S	PO	syn.	F
H. phillipsii Harv.	Stirling Range, W.A. ex M.H.	9–12	10	15–17	16	S	O	longi.	+
H. robustum Endl. Fig. 82	Darling Range, W.A. ex M.H.	10–12	11	16–20	17	S	O	longi.	+
JOSSINIA Commers. (4)									
J. aherniana Merr. Fig. 27	Philip. Nat. Herb. 9568 ex A.A.	9–10	9	14–18	16	S	O	syn.; longi.	F
J. desmantha Diels. Fig. 28	Port Moresby, Papua. Brass 885, 1926 ex K.	9–11	10	15–18	17	S	O	longi.	F
KUNZEA Reichb. (8)									
K. ambigua Druce	Wilson's Promontory, Vic.	11–14	13	14–17	16	S	SO	syn.	–
K. muelleri Benth. Fig. 64	Mt. Kosciusko, N.S.W. ex M.U.H.	7–10	8	15–23	21	S	PO	syn.	F
K. parvifolia Schau.	Grampians, Vic. ex M.U.H.	8– 9	9	16–20	17	S	O	syn.	–
LAMARCHEA Gaud. (8)									
L. hakeaefolia Gaud. Fig. 68	Locality not specified ex M.H.	13–14	14	28–32	30	S	PO	para.	+
LEPTOSPERMUM Forst. (8)									
L. attenuatum Sm. Fig. 61	Nr. Frazer's Ck., N.S.W. ex S.H.	8– 9	9	13–16	14	S	O	syn.	F
L. citratum (F. M. Bail. & C. T. White) Challinor, Cheel, & Penfold	Caprinanhurt. Coll. Cheel 1916 N.S.W. ex S.H.	7–10	9	11–14	13	S	O	syn.	F
L. coriaceum Cheel	Cheltenham, Vic. ex M.U.H.	9–11	10	18–20	19	S	O	syn.	F
L. laevigatum F. Muell.	Seaford, Vic. Coll. K. M. Pike	7–14	10	14–20	17	S	O	syn.	F

TABLE 1 (*Continued*)

Material Examined		Pollen Morphology							
Genus and Species	Source of Material	Polar Dia. (μ)		Equatorial Dia. (μ)		Shape		Colpi	Pattern
		Range	Average	Range	Average	Sides of Amb	Class		
LEPTOSPERMUM (*Continued*)									
L. myrsinoides Schl.	Oakleigh, Vic. ex M.U.H.	10–11	11	14–16	15	S	O	syn.	F
L. myrtifolium Sieb. ex Spreng.	Delegate, N.S.W. ex S.H.	9–12	10	13–17	15	S	O	syn.	F
L. rupestre Hook.	Mt. Field, Tas. ex M.U.H.	9–11	10	14–16	15	S	O	syn.	F
L. scoparium Forst. Fig. 62	Cult. Botanic Gardens, Melbourne	9–12	11	12–14	14	S	O	syn.	F
L. speciosum Schau.'	Broadwater, N.S.W. ex S.H.	9–11	10	13–16	14	S	O	syn.	F
L. sphaerocarpum Cheel	Clarence Tunnel, N.S.W. ex S.H.	9–11	10	12–16	13	Cc. S	O	syn.	F
L. squarrosum Soland. ex Gaertn.	Epping, N.S.W. ex S.H.	10–11	11	13–16	14	Cc. S	O	syn.	F
L. whitei Cheel var. *angustifolium* C. T. White	C. T. White No. 7109, S.E. Qld. ex S.H.	6– 7	7	10–12	11	S	O	syn.	F
LHOTZKYA Schau. (11)									
L. alpestris J. M. Black. Fig. 83	Cult. Botanic Gardens, Melbourne	8–14	10	12–15	14	Cc.	O	syn.	–
L. genetylloides F. Muell.	Grampians, Vic. ex M.U.H.	8–10	9	10–13	11	Cc.	O	syn.	–
LOPHOMYRTUS Burret (2)									
L. bullata (Soland.) Burret. Fig. 5	Nr. Huntersville, N.Z. ex S.H.	8–10	9	15–17	16	S	O	longi.	+
L. obcordata (Hook.) Burret	Rotorua, N.Z. Wood 28470 ex S.H.	5– 7	6	14–18	16	S Cv.	PO	longi.	+
L. ralphii (Hook. f.) Burret	Nth. I., N.Z. ex S.H.	8– 9	9	13–16	13	S	O	longi.	+
LUMA A. Gray (3)									
L. myrtoides (Berg.) Burret. Fig. 21	Brazil, Coll. Sellow. ex K.	9–11	10	16–18	17	S	O	longi.	+
LYSICARPUS F. Muell. (6)									
L. ternifolius F. Muell. Fig. 43	Morven, Qld. ex S.H.	8– 9	8	11–15	12	S	O	?	–
MEARNSIA Merr. (6)									
M. ramiflora Diels var. *humilis* Fig. 49	Kanehira & Hatusima 13113, Neth. N. Guinea ex A.A.	9–11	10	16–18	17	S	O	para.	F

MELALEUCA L. (8)									
M. odnata Turcz. var. *aspera* Cheel	Yelarbon, Qld. ex S.H.	6– 7	6	11–14	13	S	O	syn.	F
M. ericifolia Sm.	Flemington, N.S.W. ex S.H.	7– 9	8	14–17	16	S	O	syn.	F
,, ,,	Myall River, N.S.W. ex M.U.H.	11–14	13	17–20	18	S	O	syn.	F
M. erubescens Otto	Guildford, N.S.W. Coll. Blakely ex S.H.	9–11	10	13–17	16	S	O	syn.	F
M. pauciflora Turcz. Fig. 66	Jervis Bay, N.S.W. ex M.U.H.	10–13	12	18–23	21	S	O	syn.	F
M. pubescens Schau.	Silvan, Vic. ex M.U.H.	9–13	11	14–18	16	S	O	syn.	F
M. radula Lindl.	Coll. S. L. Duigan, W.A.	14–20	16	22–28	24	S	O	syn.	F
M. squamea Labill. Fig. 67	Wentworth Falls, N.S.W. ex S.H.	6– 7	7	23–27	25	S	PO	syn.; para.	F
,, ,,	Locality not specified ex M.U.H.	9–18	12	23–29	28	S	PO	syn.; para.	F
M. squarrosa Donn.	Oakleigh, Vic. ex M.U.H.	10–13	11	18–23	21	S	O	syn.; para.	F
METROSIDEROS Banks (6)									
M. excelsa Soland. Fig. 40	Coll. I. C. Cookson N.Z. 1947	11–14	13	18–21	19	S	O	para.	F
M. leptopetala F. Muell.	Bulladelah, N.S.W. ex M.U.H.	6– 8	7	18–22	21	S	PO	para.	F
M. lucida A. Rich.	Locality not specified ex M.U.H.	9–14	11	16–20	19	S	O	para.	F
M. parviflora C. T. White. Fig. 41	Type specimen ex Q.H.	6– 7	7	9–11	11	S	O	?	F
M. salomonensis C. T. White. Fig. 39	Brass 3336, Solomon Is. ex A.A.	9–11	10	16–18	17	S	O	para.	F
M. scandens Soland.	Locality unknown	10–12	11	14–18	17	S	O	para.	F
MICROMYRTUS Benth. (11)									
M. ciliatus J. M. Black. Fig. 87	Cult. Botanic Gardens, Melbourne	8–10	9	13–15	14	S Cv.	O	syn.	—
M. drummondii Benth.	Southern Cross, W.A. ex M.H.	8– 9	9	12–14	13	Cv.	O	para.	—
MYRRHINIUM Schott (2)									
M. rubriflorum (Camb.) Berg. Fig. 13	Brazil ex M.H.	9–11	10	20–23	21	S	O	para.	+
MYRTASTRUM Burret (2)									
M. rufopunctatum (Panch. ex Brongn. & Gris.) Burret. Fig. 17	Coll. Prony, New Caledonia ex S.H.	10–11	10	18–21	20	S	O	longi.	+
OCTAMYRTUS Diels (2)									
O. behrmannii Diels. Plate 1, Fig. 1	Brass 1067, Papua ex A.A.	29–32	30	40–50	46	Cc.	O	longi.	+
O. lanceolata C. T. White Fig. 20	Brass 7701, Papua ex A.A.	31–34	32	35–43	35	Cc.	SO	longi.	+

TABLE 1 (*Continued*)

Material Examined		Pollen Morphology							
Genus and Species	Source of Material	Polar Dia. (μ)		Equatorial Dia. (μ)		Shape		Colpi	Pattern
		Range	Average	Range	Average	Sides of Amb	Class		
OSBORNIA F. Muell. (5)									
O. octadonta F. Muell. Fig. 37	Port Essington, N.A. ex S.H.	11–14	12	16–18	17	S Cv.	O	syn.	F
,, ,,	Locality unknown ex M.H.	9–14	11	17–25	20	S	O	syn.	F
PHYMATOCARPUS F. Muell. (9)									
P. porphyrocephalus F. Muell. Fig. 72. Plate 1, Fig. 6	W.A. ex M.H.	8–11	9	22–25	23	S	PO	syn.	+
PILEANTHUS Labill. (11)									
P. filifolius Meissn. Fig. 90	Upper Irwin River, W.A. ex M.H.	—	14	—	30	S	PO	brevi.	–
P. peduncularis Endl. Fig. 89. Plate 1, Fig. 12	Kennedy Range, W.A. ex M.H.	—	27	—	43	S	O	longi.	–
PILIDIOSTIGMA Burret (2)									
P. glabrum Burret. Fig. 19	S.H. No. 22347	13–16	15	27–32	28	S Cv.	PO	longi.; para.	+
P. rhytisperma (F. Muell.) Burret	Mt. Archer, Qld. ex S.H. No. 16174	16–18	17	20–23	21	S Cv.	O	longi.	+
,, ,,	Lamington Plateau, Qld. Coll. S. L. Duigan	14–21	17	25–31	28	S Cv.	O	longi.	+
PILIOCALYX Brongn. & Gris. (4)									
P. baudouinii Brongn. & Gris. Fig. 33	New Caledonia ex S.H. No. 18895	14–16	15	16–20	19	S Cv.	SO	syn.	–
P. wagapensis Brongn. & Gris. Fig. 34	New Caledonia ex S.H. No. 18896	10–13	11	14–18	16	S Cv.	O	syn.	–
PIMENTA Lindl. (2)									
P. officinalis Berg. Fig. 18	Cult. Peredeniya, Ceylon ex M.H.	11–14	13	16–19	18	Cv.	O	—	+

PLEUROCALYPTUS Brongn. & Gris. (6)									
P. deplanchei Brongn. & Gris. Fig. 48	New Caledonia ex S.H. No. 18892	10–12	11	19–20	20	S	O	syn.	F
PSILOXYLON Thou. ex Tul.									
P. maritianum Baill.	Bouton, Mauritius ex K.	10–13	11	16–18	17	Cv.	O	para.	F
REGELIA Schau. (9)									
R. ciliata Schau. Fig. 73	Lower Canning River, W.A. ex S.H.	11–14	13	18–23	21	Cc. S	O	para.	F
,, ,,	W.A. ex M.H.	11–15	14	25–28	27	Cc.	O	para.	+
R. grandiflora Benth. Fig. 74	Cult. Ivanhoe, Vic. ex M.H.	17–20	19	31–36	34	Cc.	O	para.	+
R. inops Schau. Fig. 75	King George Sound, W.A. ex M.H.	12–16	15	29–36	32	S	PO	syn.	F
RHODAMNIA Jack (2)									
R. argentea Benth.	Locality not specified ex M.H.	9–11	10	15–17	16	S	O	longi.	+
R. dumetorum (Poir.) Merr. & Perry	Locality not specified ex A.A.	10–12	11	15–17	16	S	O	longi.	+
R. maideniana C. T. White. Fig. 2	MacPherson Range, Qld. ex Q.H.	9–11	10	14–16	15	S	O	longi.	+
R. propinqua C. T. White	Brass 8592, Papua ex A.A.	10–12	11	16–18	17	S	O	longi.	+
R. spongiosa C. T. White	Coll. S. L. Duigan, Qld.	10–12	11	16–18	17	S	O	longi.	+
R. trinervia Bl.	Coff's Harbour, N.S.W. ex S.H.	7–11	9	18–22	19	S	PO	longi.	+
,, ,,	Qld. ex M.H.	8–11	10	17–22	20	S	O	longi.	+
RHODOMYRTUS DC. (2)									
R. becklerii (F. Muell.) Sm.	Locality not specified ex M.H.	13–18	17	22–27	23	S Cv.	O	longi.	+
R. macrocarpa Benth.	Kamerunga Nursery, Qld. ex S.H.	15–18	17	26–29	25	S Cv.	O	longi.	+
,, ,,	Locality not specified ex M.H.	18–23	19	29–34	31	S Cv.	O	longi.	+
R. obovata C. T. White	Brass 8678, Papua ex A.A.	18–22	20	27–31	29	S Cv.	O	longi.; para.	+
R. psidioides (Don.) Benth. Fig. 15	Murwillumbah, N.S.W. ex S.H.	9–11	10	23–27	25	S Cv.	PO	longi.	+
,, ,,	Myall Lakes, N.S.W. ex M.U.H.	11–17	15	22–30	27	S Cv.	O	longi.	+
R. tomentosa (Ait.) Hassk.	Locality not specified ex A.A.	14–16	15	20–23	21	S	O	longi.	+
R. trineura F. Muell. Plate 1, Fig. 3	Locality not specified ex A.A.	15–19	18	22–27	24	S	O	longi.	+

TABLE 1 (*Continued*)

Material Examined		Pollen Morphology							
Genus and Species	Source of Material	Polar Dia. (μ)		Equatorial Dia. (μ)		Shape		Colpi	Pattern
		Range	Average	Range	Average	Sides of Amb	Class		
Scholtzia Schau. (10)									
S. ladiflora Benth.	Canning Plains, W.A. ex S.H.	6– 9	7	10–12	11	S	O	syn.	–
S. laxiflora Benth.	W.A. Coll. Drummond 1854 ex S.H.	7– 9	8	10–13	11	S	O	syn.	–
S. leptantha Benth.	Shark's Bay, W.A. ex S.H.	7– 9	8	11–14	13	S	O	syn.	–
S. obovata Schau. Fig. 80	Forrest Field, Perth, W.A. ex S.H.	7–10	9	8–11	10	S	SO	syn.	F
Spermolepis Brongn. & Gris. (6)									
S. gummifera Brongn. & Gris. Fig. 42	New Caledonia. Franc No. 243 ex. K.	6– 7	7	10–12	11	S	O	syn.	–
,, ,,	New Caledonia. Franc No. 243 ex B.M.	6– 7	7	10–12	11	S	O	syn.	–
Stereocaryum Burret (4)									
S. rubiginosum (Brongn. & Gris.) Burret. Fig. 23	New Caledonia ex M.H.	9–12	11	17–20	18	S	O	syn.	+
Syncarpia Ten. (6)									
S. glomulifera (Sm.) Ndz.	Casins Dist., N.S.W. ex S.H.	10–12	11	14–16	16	S	O	syn.; ?para.	F
S. hillii F. M. Bail. Fig. 46	Locality not specified ex Q.H.	11–12	11	14–17	16	S	O	syn.	F
S. procera (Salisb.) Domin	New South Wales ex M.H.	14–18	15	16–21	19	S	SO	syn.	F
,, ,,	Parramatta River, N.S.W. ex M.U.H.	8–14	11	16–20	18	S	O	para.	F
Syzygium Gaertn. (4)									
S. corticosum (Lour.) Merr. & Perry	Clemens 3532 ex A.A.	6– 7	7	9–11	10	S	O	para.	–
S. ventenatii Merr. & Perry. Fig. 31	Port Macquarie, N.S.W. ex S.H.	6– 7	7	13–16	14	S	O	para.	–

Syzygium (*Continued*)									
S. ventenatii Merr. & Perry.	Cult. Botanic Gardens, Melbourne	7– 9	8	13–16	14	S	O	para.	–
S. zeylanicum (L.) DC. Fig. 30	Rahmat Si Toroes 2296 ex A.A.	6– 8	7	12–16	14	S	O	para.	–
Tepualia Griseb. (6)									
T. stipularis Griseb. Fig. 45. Plate 1, Fig. 11	Chili. Coll. H. J. Elwes, ex K.	10–12	11	20–22	21	S	O	para.	–
Thryptomene Endl. (11)									
T. calycina Stapf	Cult. Botanic Gardens, Melbourne	7– 9	8	12–15	14	S	O	brevi.	–
T. maisonneuvii F. Muell. Fig. 92	Ashburton River, W.A. ex M.H.	9–10	9	13–15	14	S	O	brevi.	–
T. saxicola Schau.	Kalgan River, W.A. ex M.H.	9–11	10	13–16	15	S Cv.	O	brevi.	–
Tristania R. Br. (6)									
T. conferta R. Br. Fig. 52	Cult. Cheltenham, N.S.W. ex S.H.	7–10	9	12–14	13	S	O	syn.; para.	–
,, ,,	Bulladelah, N.S.W. ex M.U.H.	8–11	10	14–18	16	S	O	syn.; para.	–
T. laurina R. Br.	Coramba, N.S.W. ex S.H.	5– 6	6	11–14	12	S	PO	para.	–
T. neriifolia R. Br. Fig. 53	Blue Mtns., N.S.W. ex M.H.	4 –5	5	6– 7	7	Cc. S	O	?syn.	–
,, ,,	Hornsby, N.S.W. ex M.U.H.	4– 5	5	5– 7	6	S Cv.	O	syn.	–
T. suaveolens Sm.	Morton Bay, Qld. ex M.U.H.	7– 9	8	12–16	14	S	O	syn.; para.	–
Ugni Turcz. (2)									
U. molinae Turcz. Fig. 3	Locality not specified, ex M.H.	14–16	15	16–23	21	S Cv.	O	longi.	+
Uromyrtus Burret (2)									
U. artensis (Montr.) Burret. Fig. 12	New Caledonia, Coll. Vieillard, No. 539, ex M.H.	8– 9	9	11–13	12	Cc. S	O	para.	F
U. emarginata (Panch. ex Brongn. & Gris.) Burret. Fig. 11	Herb. J. Franc., Noumea ex M.H.	8– 9	9	11–14	13	S Cv.	O	?longi.	F
Verticordia DC. (11)									
V. chrysantha Endl.	Locality not specified, ex M.U.H.	18–23	21	19–23	20	S	PS	brevi.	–
V. densiflora Lindl. Fig. 97	King George Sound, W.A. ex S.H.	14–18	16	18–23	20	S Cv.	SO	brevi.	F
V. grandiflora Endl.	Nr. Perth, W.A. ex M.U.H.	23–29	27	23–27	26	S	PS	brevi.	F
V. grandis Drum.	Mingenew, W.A. ex M.H.	14–20	18	23–28	26	S	O	para.	F

TABLE 1 (*Continued*)

Material Examined		Pollen Morphology							
Genus and Species	Source of Material	Polar Dia. (μ)		Equatorial Dia. (μ)		Shape		Colpi	Pattern
		Range	Average	Range	Average	Sides of Amb	Class		
WEHLIA F. Muell. (11)									
W. coarctata F. Muell.	Coolgardie, W.A. ex S.H. No. 23534	9–11	10	17–20	18	S Cv.	O	syn.	F
W. staminosa F. Muell.	Mt. Hale, W.A. ex M.H.	11–15	14	24–27	25	S Cv.	O	syn.; para.	+
W. thryptomenioides F. Muell. Fig. 88	Victoria Desert, W.A. ex M.H.	13–15	14	20–23	22	S	O	syn.	+
XANTHOMYRTUS Diels (2)									
X. papuana var. *parviflora* Merr. & Perry. Fig. 10	Brass 1933, No. 4573 ex Q.H.	7–11	9	14–16	15	S	O	longi.	+
Xanthostemon F. Muell. (6)									
X. crenulatus C. T. White Fig. 47	Papua. Brass No. 8358 ex Q.H.	11–13	12	14–17	16	Cc S	SO	syn.;	F
X. paradoxus F. Muell.	Northern Territory, Aust. ex S.H.	9–11	11	18–23	20	S	PO	para.	F
X. verdugonianus Naves	Philippines ex S.H. No. 18894	11–14	13	16–20	18	S	O	syn.; para.	F

TABLE 2

POLLEN MORPHOLOGICAL CHARACTERS OF SOME EUCALYPTUS SPECIES

F denotes that the pattern is so pale that the exine surface appears faintly flecked

Species of *Eucalyptus*	Characters of Pollen Grains									
	Polar Dia. (μ)		Equatorial Dia. (μ)		Sides of Amb			Apocolpia	Pattern	Exine thickened at Angles
	Range	Average	Range	Average	Concave	Straight	Convex			
aggregata Deane & Maid.	10–13	11	16–18	17		+	+	+	–	–
alpina Lindl.	14–16	15	18–23	20		+		+	–	+
brachyandra F. Muell. Fig. 59	7– 9	8	12–14	14	+	+		+	–	–
caesia Benth.	14–16	15	23–27	25		+		+	+	–
caleyi Maid.	12–14	13	18–20	19		+		+	–	–
camaldulensis Dehn.	9–12	11	16–20	19		+		+	–	±
capitellata Sm.	14–15	14	22–25	24		+		+	–	+
cinerea F. Muell.	14–16	15	22–25	23		+		+	–	+
coccifera Hook. f.	11–14	12	19–20	20		+		+	F	–
deglupta Bl.	9–12	11	18–20	19				+	+	–
" "	9–11	10	14–18	16	+	+		+	–	±
diversicolor F. Muell.	13–16	14	20–23	22		+	+	+	–	–
dives Schau.	13–15	14	18–23	19		+		+	–	±
dumosa A. Cunn.	14–16	15	20–23	22		+		+	F	+
elaeophora F. Muell.	11–14	13	18–22	20		+		+	F	±
erythrocorys F. Muell.	14–17	15	28–32	30		+		+	F	–
fruticetorum F. Muell.	11–16	14	18–25	21			+	+	–	±
gigantea Hook. f.	12–16	15	20–25	24		+		+	F	+
globulus Labill. Fig. 57	12–16	14	25–29	26		+		+	F	+
"	13–16	14	25–29	27		+		+	–	+
"	14–18	15	25–28	27	+	+	+	+	–	+
gomphocephala DC.	14–18	16	25–27	25		+		+	F	±

TABLE 2 (*Continued*)

Species of *Eucalyptus*	Characters of Pollen Grains									
	Polar Dia. (μ)		Equatorial Dia. (μ)		Sides of Amb			Apocolpia	Pattern	Exine thickened at Angles
	Range	Average	Range	Average	Concave	Straight	Convex			
goniocalyx F. Muell.	11–14	13	22–25	23		+		+	–	±
gracilis F. Muell.	11–14	13	18–20	19		+	+	–	–	–
gummifera (Gaertn.) Hochr.	23–27	26	29–36	33		+		+	–	–
gunnii Hook.	9–12	11	18–20	19		+		+	–	+
haemastoma Sm.	10–12	11	16–18	18		+		+	F	+
hemiphloia F. Muell.	13–16	15	18–23	21		+		+	–	–
incrassata Labill.	15–19	18	23–27	25		+		+	F	–
kitsoniana (J. G. Lueh.) Maid.	10–14	11	19–21	20		+	+	+	F	+
lehmanni Preis.	13–16	14	21–24	23	+	+		+	–	+
leptophylla F. Muell. Fig. 60	6– 7	7	10–14	11		+		+	–	–
leucoxylon F. Muell.	11–14	12	18–20	20		+	+	+	–	–
ligustrina DC.	9–11	10	16–19	18		+		+	F	+
longifolia Link & Otto	11–14	12	23–27	25		+		+	–	+
macrocarpa Hook.	12–16	15	25–28	26		+		+	+	–
,,	11–14	14	16–20	19		+		+	–	+
macrorrhyncha F. Muell.	11–14	12	20–24	22		+		+	F	+
maculata Hook.	18–20	20	29–34	30		+		+	–	+
maideni F. Muell.	14–19	15	25–27	26		+		+	–	+
melliodora A. Cunn.	9–11	10	15–18	16		+	+	+	–	–
microcorys F. Muell.	11–13	12	16–18	17	+	+		–	+	–
microtheca F. Muell.	14–16	14	20–23	22		+		+	F	+
miniata A. Cunn. Fig. 56. Plate 1, Fig. 4	14–18	15	34–36	35		+		+	+	–
mitchelliana Camb.	12–14	13	20–24	22		+		+	+	±

TABLE 2 (*Continued*)

Species of *Eucalyptus*	Characters of Pollen Grains									
	Polar Dia. (μ)		Equatorial Dia. (μ)		Sides of Amb			Apocolpia	Pattern	Exine thickened at Angles
	Range	Average	Range	Average	Concave	Straight	Convex			
muelleriana Howitt	12–14	13	23–29	25	+	+		+	—	+
nowraensis Maid.	16–22	19	27–31	29		+		+	—	—
obliqua L'Herit.	13–14	14	22–27	23		+		+	F	+
odontocarpa F. Muell.	11–14	13	18–20	19		+		±	F	—
odorata Behr & Schlecht.	12–14	13	18–21	19	+	+		±	—	—
oleosa F. Muell.	11–14	12	19–21	20			+	±	—	±
ovata Labill.	11–14	13	22–25	24		+		+	F	±
pachyphylla F. Muell.	11–16	14	18–23	20		+		+	—	+
paniculata Sm.	11–13	12	16–20	18	+	+		—	F	—
papuana F. Muell.	12–14	13	18–20	18		+		+	—	—
,,	11–12	12	18–22	19	+			+	—	—
pauciflora Sieb.	12–14	13	21–23	22		+		+	F	F
perfoliata R. Br.	21–25	24	31–34	33		+		+	F	—
pilularis Sm.	11–14	13	22–23	22		+		+	+	+
piperita Sm.	11–13	12	21–25	23		+		+	F	+
planchoniana F. Muell.	18–20	19	27–30	29		+		+	+	—
polyanthemos Schau.	9–14	12	15–18	17		+		+	—	—
populifolia Hook.	8–12	11	16–20	18				—	—	—
pyriformis Turcz.	14–16	14	22–25	23	+	+		+	+	—
pyriformis var. *elongata* Maid.	9–11	10	18–23	19		+	+	+	—	+
regnans F. Muell. Fig. 58	10–14	13	20–23	22				+	+	+
resinifera Sm.	9–12	11	16–20	19		+		+	F	+
rubida Deane & Maid.	9–11	10	18–20	19		+		+	—	+
saligna Sm.	14–17	15	20–23	22		+		+	—	—

TABLE 2 (*Continued*)

Species of *Eucalyptus*	Characters of Pollen Grains									
	Polar Dia. (μ)		Equatorial Dia. (μ)		Sides of Amb			Apocolpia	Pattern	Exine thickened at Angles
	Range	Average	Range	Average	Concave	Straight	Convex			
scabra Dum-Cours	11–14	12	20–23	22	+	+		+	—	+
setosa Schau. Plate 1, Fig. 2	18–24	22	27–34	31		+		—	±	±
siderophloia Benth.	16–20	18	23–27	25		+		+	F̄	±
sideroxylon A. Cunn.	12–16	14	20–23	22	+	+		+	—	—
,,	9–14	11	18–23	21		+		+	—	+
smithii R. T. Baker	9–12	11	22–25	23		+		+	F̄	—
stricta Sieb.	14–16	15	23–27	25		+		+	+	+
stellulata Sieb.	14–16	15	22–27	24		+		+	F̄	+
stuartiana F. Muell.	12–14	14	20–26	23		+		+	—	+
terminalis F. Muell.	22–25	24	29–33	30		+		+	—	—
tesselaris F. Muell.	7–10	9	16–20	18		+		+	+	—
tetrodonta F. Muell.	15–18	16	25–28	27		+		+	+	+
torquata J. G. Lueh.	16–19	18	25–29	27		+		+	—	±
umbellata (Gaertn.) Domin	14–16	15	21–25	23		+		+	—	+
uncinata Turcz.	11–14	12	16–20	18		+		+	—	—
vernicosa Hook. f.	12–14	13	20–25	22		+		+	F̄	±
viminalis Labill.	11–14	12	20–23	22		+		+	F̄	+
viridis R. T. Baker	11–14	12	16–18	17		+		—	—	+
watsoniana F. Muell.	11–13	11	18–20	19		+		±	—	—

The nomenclature adopted for the descriptive morphology of the pollen is that suggested by Erdtman (1952) in his book "Pollen Morphology and Plant Taxonomy". A glossary of the terms used in the present paper is given in Section IX.

II. HISTORICAL

References to the earlier descriptions and illustrations of pollen grains of the Myrtaceae are listed by Selling (1947).

Amongst the first records are drawings contained in the unpublished work of Francis Bauer, housed at the British Museum (Natural History). Bauer's illustrations include pollen grains of some species of *Eucalyptus* and *Melaleuca*, and are believed to have been made at Kew between 1790 and 1840 (Wodehouse 1935).

von Mueller (1879) recorded measurements of the grains of 48 species of *Eucalyptus*; these were probably made from fresh material. The results obtained in the present survey, after treatment of the pollen by the acetolysis method, have shown little variation from von Mueller's original figures.

Erdtman (1952) described the grains of 19 species after investigating those of 45 species from 30 genera. This is the most comprehensive palynological review of the family to date.

III. METHOD

Wherever possible, mature buds or flowers of herbarium specimens were used in preference to living material, to ensure greater accuracy in identification of the material used.

The pollen was treated by the acetolysis method (Erdtman 1943) and mounted in glycerine jelly. Usually both safranin-stained and unstained mounts were prepared, and sometimes a portion of the grains was bleached by chlorination.

In Tables 1 and 2 the values for the equatorial and polar diameters give the range for, and average of, 10 measurements. These values thus give an approximate guide to the size of the grains. The sculpture is included in the overall dimensions, as it is too shallow to permit separate treatment.

IV. TAXONOMY

Since Niedenzu's original classification of the Myrtaceae was proposed, a number of new genera has been added, concepts of older genera have been changed or modified, and the precise limits of certain other genera are still disputed by taxonomists.

A certain amount of taxonomic confusion exists concerning the correct interpretation of the genus *Eugenia* L. Ingle and Dadswell (1953) have summarized the many differing diagnoses of *Eugenia* as follows: "Niedenzu (1893) in his classification of the various genera within the Myrtaceae restricted *Eugenia* L. to the tropical American species, and placed the great bulk of the Old World *Eugenia* species in *Syzygium* Gaertn. and *Jambosa* DC. Merrill and Perry accept one very large Old World genus, *Syzygium* Gaertn. (including *Jambosa* DC. and *Caryophyllus* L.); in addition, they have reinstated and revised *Cleistocalyx* Bl., and suggested that *Acmena* DC. is a valid genus (1937, 1938*a*). Both *Cleistocalyx* and *Acmena* are restricted to the Old World. Merrill has recently (1950*b*) followed Diels by accepting *Jossinia* Commers. to cover a small residue of Old World species which resembles certain of the American *Eugenia* species much more closely than they do the Old World *Syzygium* species. Other botanists (e.g. Henderson 1949) do not agree, and retain all the Old World species in *Eugenia* L.; others, while accepting *Syzygium* Gaertn. as distinct from *Eugenia* L., object to the separation of small genera such as *Cleistocalyx* and *Acmena* from *Syzygium* (Airy Shaw 1949 in Merrill 1950*b*)."

In the present account the views expressed by Merrill and Perry (1937, 1938*a*) and Merrill (1950) have been accepted, more because of evidence from pollen morphology than because of any knowledge of the botanical principles involved. Differences in the pollen grains examined seem sufficiently consistent to justify Merrill and Perry's concept of maintaining *Syzygium*, *Acmena*, and *Cleistocalyx* as separate genera, rather than adopting the broader views of Henderson or Airy Shaw.

When considering the wood anatomy of *Eugenia* as a whole, Ingle and Dadswell (1953) divided the genus into two groups, "*Eugenia* A, covering the few species from the Pacific region which agree anatomically with the New World species (it is possible that botanically some or all of these species fall in *Jossinia* Commers.); and *Eugenia* B, covering *Syzygium* and those species similar in wood anatomy, but for which new combinations have not yet been made." The three genera *Syzygium*, *Acmena*, and *Cleistocalyx* were placed together in *Eugenia* B. since they are very close wood anatomically.

Pollen morphology supports the grouping based on wood structure, in that pollen grains of the available species of *Eugenia* A (with the exception of *Eugenia stricta* Panch., which will be considered later) are distinct from those of *Eugenia* B, and more or less agree with those of *Jossinia*.

In the present account, species listed in Table 1 under *Eugenia* have been separated into *Eugenia* A and *Eugenia* B, as recognized by Ingle and Dadswell. It is probable that all the *Eugenia* B species should more correctly be placed in *Syzygium*, since Merrill and Perry (1938*b*) suggest that *Syzygium* should include "most of the Old World species of *Eugenia*". However, until new combinations are made, these species must temporarily remain under *Eugenia*. In Table 1, therefore, species belonging to Ingle and Dadswell's *Eugenia* B appear under *Acmena*, *Cleistocalyx*, *Eugenia* B (probably *Syzygium*) and *Syzygium*.

Burret (1941*a*, 1941*b*) has assigned all species in the south-west Pacific area previously included in *Myrtus* L. to a number of new genera, so that *Myrtus* (sens. str.) is now no longer represented in this region. Of these new combinations material of the following genera has been studied: *Austromyrtus* Burret, *Lophomyrtus* Burret, *Myrtastrum* Burret, *Pilidiostigma* Burret, *Rhodomyrtus* DC., and *Uromyrtus* Burret.

Eugenia stricta Panch. ex Brongn. & Gris. has been transferred by Burret to ? *Austromyrtus stricta*. Ingle and Dadswell (1953) remark that the wood anatomy of the "sparse material" studied by them is closer to that of *Eugenia* (sens. str.) than to *Austromyrtus*, and they have considered it under the heading of *Eugenia* A. Pollen morphology, however, suggests a closer relationship with *Austromyrtus*, thus supporting Burret's transfer, and for this reason it is considered in the present paper under this name. Unfortunately, fertile material of *Eugenia horizontalis*

Panch. ex Brongn. & Gris., also transferred by Burret to *Austromyrtus*, but similar in wood anatomy to *Eugenia* A (Ingle and Dadswell 1953), was unobtainable. The late Mr. C. T. White indicated (Dadswell and Ingle 1947) that both *E. stricta* and *E. horizontalis* might be small-leaved species of *Syzygium*, but the pollen grains examined of *E. stricta* do not uphold this suggestion.

Burret's transfers of *Orthostemon* Berg. to *Acca* Berg., *Myrceugenia* Berg. to *Luma* A. Gray, and certain species of *Spermolepis* and *Calycorectes* to *Stereocaryum* Burret, have also been followed.

V. General Description of the Pollen Grains of Different Genera

A family description for pollen grains of the Myrtaceae has been given by Selling (1947) and Erdtman (1952). The following amended description is based on material studied during the present investigation.

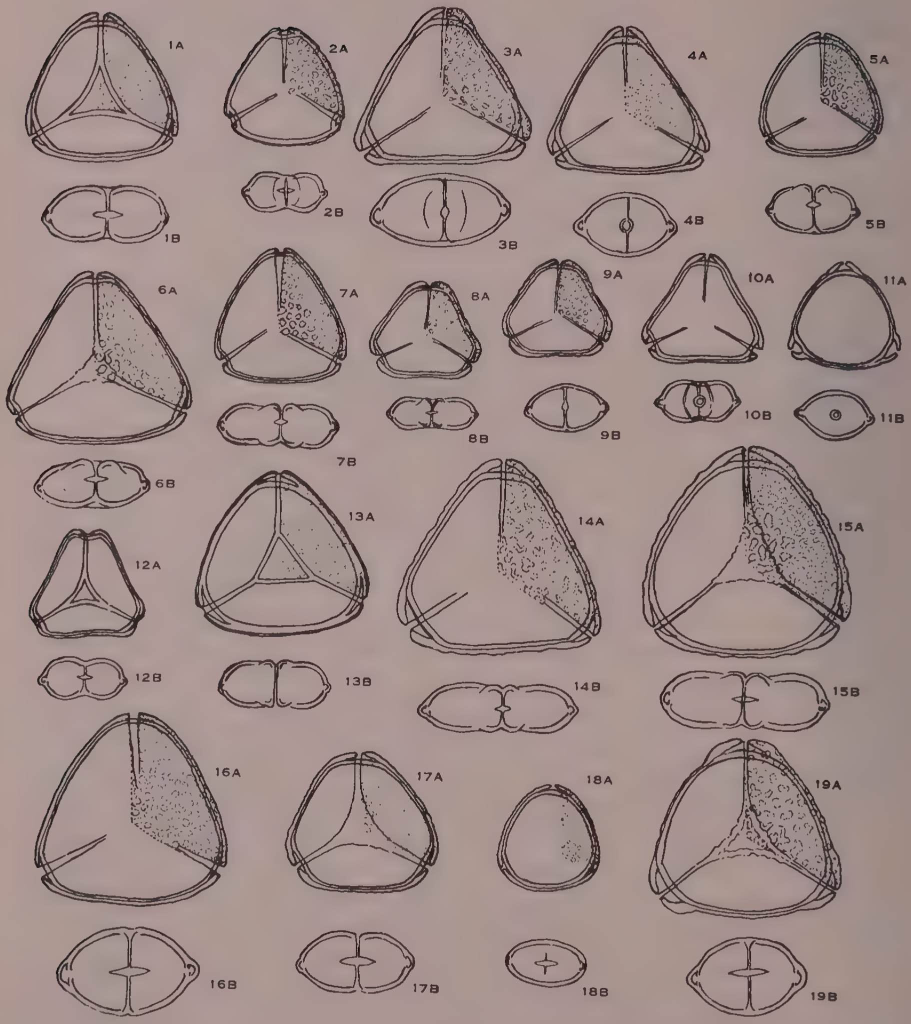
In general, the pollen grains are small to medium, radiosymmetrical, isopolar to slightly subisopolar, tricolporate (occasionally di- or tetracolporate, rarely pentacolporate), angulaperturate, oblate (sometimes peroblate or subspheroidal), syncolpate or parasyncolpate, with a triangular amb and a smooth or faintly patterned exine surface. The exine is two layered; generally the nexine is thicker than the sexine, but it may be of the same thickness or thinner.

This description applies to the grains of the majority of species studied, but there are differences that characterize certain genera or tribes, and these will be discussed below.

Erdtman (1952) has remarked that the Myrtaceae is " a ± stenopalynous family", but a greater variation than was previously envisaged has been revealed by the pollen of some rarer species. For example, Selling (1947) mentioned that the size values (of the equatorial diameter) available from previous literature range from 10 to 25 μ. The present study has extended this range to from 6 to 50 μ.

The apertures, with few exceptions, consist of an elongated furrow (colpus) at right angles to an inner, smaller aperture or os. The longitudinal furrow narrows at the polar extremities and often extensions from it continue over the polar surfaces in the form of narrow grooves. In the following descriptions these grooves are regarded as parts of the colpi and are included in that term. The colpi may meet at or near the poles (syn- or parasyncolpate, e.g. Plate 1, Figs. 6 and 4 respectively) or may disappear before reaching them (longicolpate, Plate 1, Fig. 1; brevicolpate, Plate 1, Fig. 7). Pollen grains of most members of the Chamaelaucieae are brevi- or brevissimicolpate and the ora are lalongate.

Various opinions as to the nature of the markings on the polar surfaces have been expressed. Mohl (1835), Fischer (1890), and Potonié (1934) considered them as parts of the colpi, the view adopted here and by Erdtman (1952). Selling (1947) regards them as arched lines and calls them "arci"; he defines an arcus as "a curved, band-like thickening of the exine, connecting two pores". This is in contradiction to the opinion expressed above that these markings are in the form of minute channels rather than raised lines. Cranwell (1953), when discussing the divided or Y-furrow, states that "confusion with fused furrows might occur, as with grains



Figs. 1-19.—Drawings of pollen grains in polar view *A* (magnified approx. 800 diameters), and equatorial view *B* (not drawn to scale). Fig. 1.—*Acca sellowiana*. Fig. 2.—*Rhodamnia maideniana*. Fig. 3.—*Ugni mollinae*. Fig. 4.—*Calycolpus glaber*. Fig. 5.—*Lophomyrtus bullata*. Fig. 6.—*Austromyrtus acmenioides*. Fig. 7.—*Austromyrtus tenuiifolia*. Fig. 8.—*Austromyrtus racemulosa*. Fig. 9.—*Austromyrtus stricta*. Fig. 10.—*Xanthomyrtus papuana* var. *parviflora*. Fig. 11.—*Uromyrtus emarginata*. Fig. 12.—*Uromyrtus artensis*. Fig. 13.—*Myrrhinium rubriflorum*. Fig. 14.—*Decaspermum hainanense*. Fig. 15.—*Rhodomyrtus psidioides*. Fig. 16.—*Fenzlia retusa*. Fig. 17.—*Myrtastrum rufopunctatum*. Fig. 18.—*Pimenta officinalis*. Fig. 19.—*Pilidiostigma glabrum*.

of . . . the Myrtaceae. In these types, however, the furrows run meridionally, in true dicotyledonous fashion; further, where they fuse they form "islands" of ektexine over the poles".

The pattern is usually indefinite and often so faint as to give the surface of the grains a flecked appearance. When more distinct, it appears to be a shallow reticulum, or LO-pattern as defined by Erdtman (1952), and in the glossary (Section IX).

(1) *Myrtoideae—Myrteae—Orthostemoninae*

Fig. 1

Genus examined.—*Acca* Berg. (syn. *Feijoa* Berg., *Orthostemon* Berg.).

Material of only one species of this tribe has been studied, so that no tribal comparisons can be given. Details of the pollen morphology of *Acca sellowiana* are given in Table 1.

(2) *Myrtoideae—Myrteae—Myrtinae*

Figs. 2-20

Genera examined.—*Rhodamnia* Jack; *Ugni* Turcz.; *Calycolpus* Berg.; *Lophomyrtus* Burret; *Austromyrtus* (Ndz.) Burret; *Xanthomyrtus* Diels; *Uromyrtus* Burret; *Myrtastrum* Burret; *Myrrhinium* Schott; *Decaspermum* Forst.; *Rhodomyrtus* DC.; *Fenzlia* Endl.; *Pimenta* Lindl.; *Octamyrtus* Diels; *Pilidiostigma* Burret.

The pollen grains of genera in this tribe have an LO-pattern which is often more pronounced at the poles than in the mesocolpia; usually the grains are longicolpate (Plate 1, Figs. 1, 3), but when the colpi are continuous they are parasyncolpate; the pattern is then most conspicuous in the apocolpia. Often the ora are lalongate.

Close similarities in pollen characters exist between *Rhodamnia*, *Lophomyrtus*, *Austromyrtus*, and most species of *Decaspermum*; *Ugni*, *Calycolpus*, and *Fenzlia*; *Rhodomyrtus* and *Pilidiostigma*.

The grains of *Myrrhinium* are parasyncolpate, those of *Myrtastrum* syncolpate, and those of *Pimenta* are small and rounded with no extensions to the colpi. The grains of *Octamyrtus* are easily recognized by their exceptionally large size (35-50 μ).

The limited material of *Xanthomyrtus* studied has no pattern, and does not conform to the general type for this group.

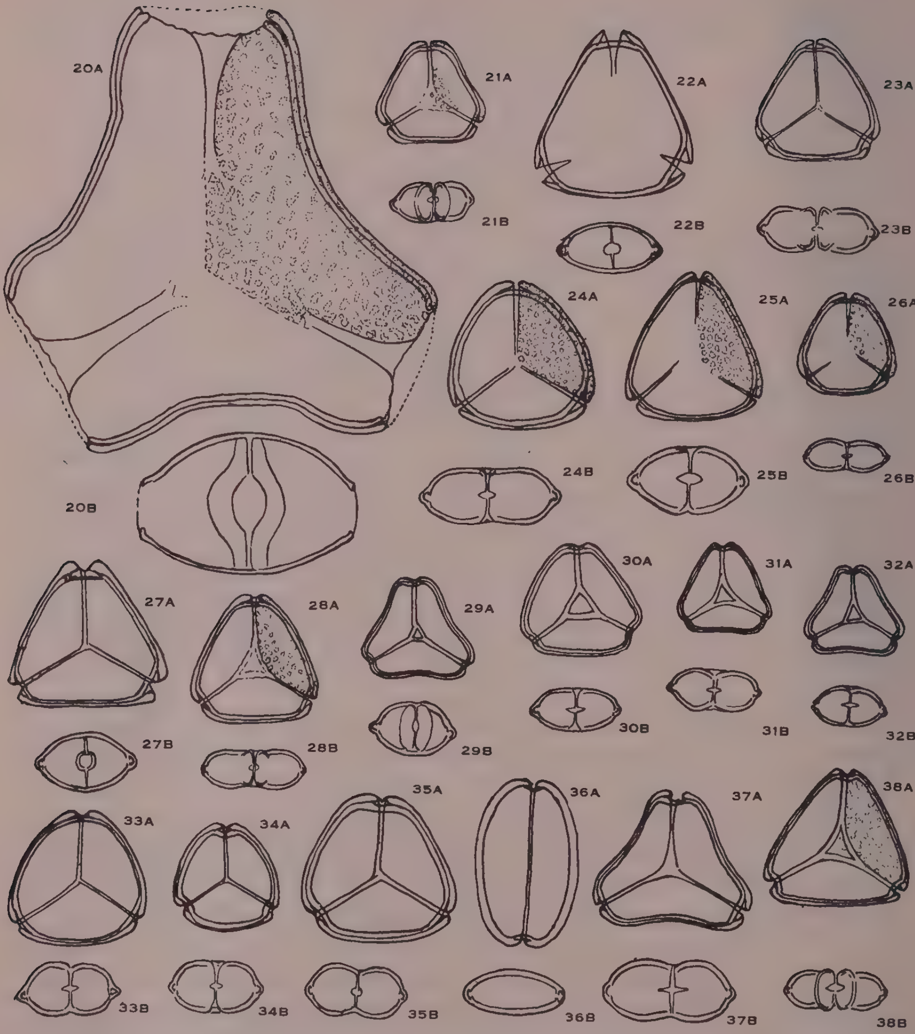
Grains of the two species of *Uromyrtus* examined are not similar to one another or to those of the other genera in this tribe. The pollen of *U. artensis* (Montr.) Burret is parasyncolpate with a smooth exine surface; that of *U. emarginata* (Panch. ex Brongn. & Gris.) Burret, is brevicolpate with a very faint exine pattern and relatively large vestibulae.

(3) *Myrtoideae—Myrteae—Myrciinae*

Figs. 21, 22

Genera examined.—*Luma* A. Gray (syn. *Myrceugenia* Berg.); *Calyptranthes* Swarz.

Grains of these two genera have features in common with those of the Myrtineae, i.e. they are longicolpate with a faint LO-pattern. The grains of *Luma myrtoides* (Berg.) Burret are closely similar to those of *Austromyrtus*.



Figs. 20-38.—Drawings of pollen grains in polar view *A* (magnified approx. 800 diameters), and equatorial view *B* (not drawn to scale). Fig. 20.—*Octamyrtus lanceolata*. Fig. 21.—*Luma myrtoides*. Fig. 22.—*Calyptranthes lucida*. Fig. 23.—*Stereocaryum rubiginosum*. Fig. 24.—*Eugenia albanensis*. Fig. 25.—*Eugenia capensis*. Fig. 26.—*Eugenia macrohila*. Fig. 27.—*Jossinia aherniana*. Fig. 28.—*Jossinia desmantha*. Fig. 29.—*Eugenia* (? *Syzygium*) *hodgekinsoniae*. Fig. 30.—*Syzygium zeylanicum*. Fig. 31.—*Syzygium ventenatii*. Fig. 32.—*Cleistocalyx seemannii*. Fig. 33.—*Piliocalyx baudouinii*. Fig. 34.—*Piliocalyx wagapensis*. Fig. 35.—*Acmena smithii*. Fig. 36.—*Acmena macrocarpa* (type). Fig. 37.—*Osbornia octadonta*. Fig. 38.—*Backhousia citriodora*.

(4) *Myrtoideae—Myrteae—Eugeniinae*

Figs. 23-35

Genera examined.—*Eugenia* L.; *Jossinia* Commers.; *Syzygium* Gaernt.; *Piliocalyx* Brongn. & Gris.; *Acmena* DC.; *Cleistocalyx* Bl. (including *Acicalyptus* A. Gray); *Stereocaryum* Burret.

Small, syncolpate (*Acmena*, *Piliocalyx*) or parasyncolpate (*Eugenia* B, *Cleistocalyx*, *Syzygium*) grains with broad apices and smooth or faintly patterned exines, are characteristic of this group.

The pollen grains of *Acmena* can be distinguished from those of *Cleistocalyx* and *Syzygium*, which themselves cannot be separated, by lack of polar islands and a more rounded amb. The three species of *Eugenia* A available have grains that resemble those of members of the Myrtinae in being longicolpate with a patterned exine. Grains of *Jossinia*, especially those of *J. desmantha*, also show a connexion with the Myrtinae-Myrciinae type.

Dicolporate and tetracolporate grains appear to be more numerous in members of this group than in other genera. In preparations of *Acmena divaricata* and *A. macrocarpa* (type specimen) all the pollen grains are bilateral and dicolporate.

The material of *Cleistocalyx gustavioides* available indicates that pollen of this species differs from that of other species of *Cleistocalyx* in both size and shape; in these features it resembles that of *Angophora*.

(5) *Leptospermoideae—Leptospermeae—Backhousiinae*

Figs. 37, 38

Genera examined.—*Osbornia* F. Muell.; *Backhousia* Hook. & Harv.

The grains of *Osbornia* (monotypic) are syncolpate with a smooth exine and lalongate ora, and are ± similar to those of *Backhousia* in shape, but the latter often have a faint pattern and can be parasyncolpate.

(6) *Leptospermoideae—Leptospermeae—Metrosiderinae*

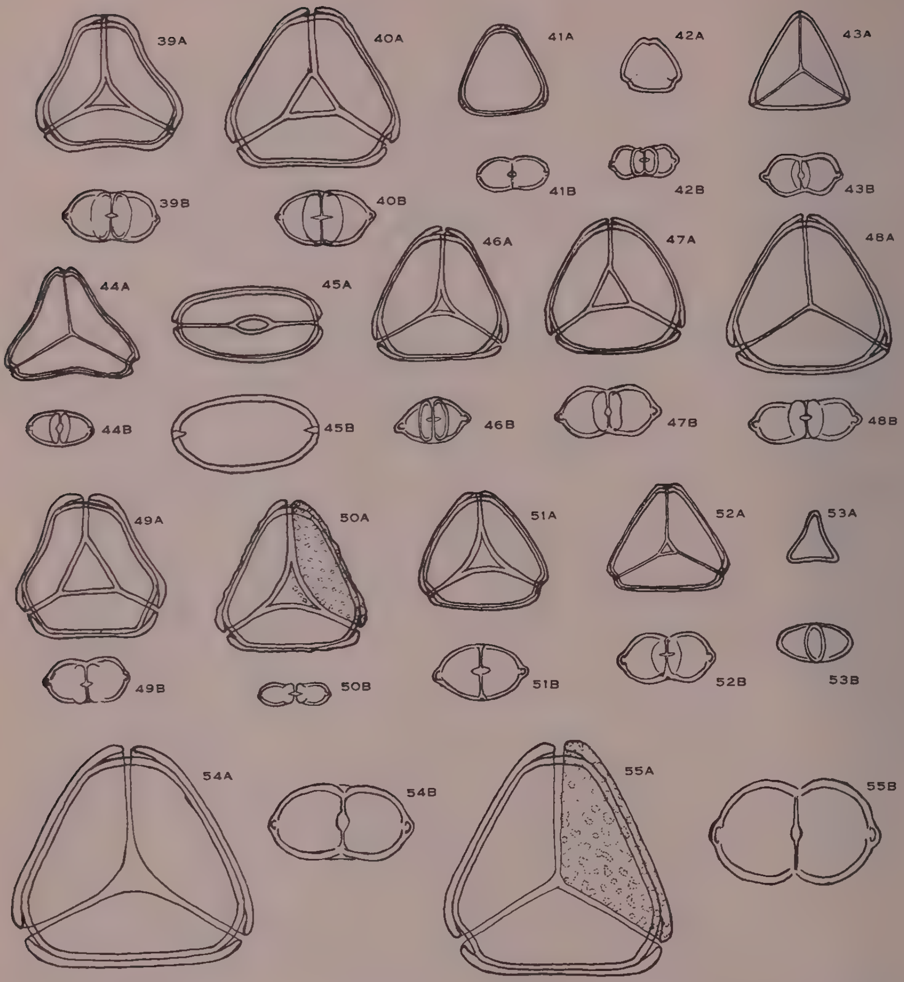
Figs. 39-52

Genera examined.—*Metrosideros* Banks; *Spermolepis* Brongn. & Gris.; *Lysicarpus* F. Muell.; *Cloezia* Brongn. & Gris.; *Tepualia* Griseb.; *Syncarpia* Ten.; *Choricarpia* Domin; *Xanthostemon* F. Muell.; *Pleurocalyptus* Brongn. & Gris.; *Eucalyptopsis* White; *Mearnsia* Merr.; *Tristania* R. Br.

Pollen of members of this group is comparatively variable. Parasyncolpate grains are common (*Metrosideros*, *Tepualia*, *Choricarpia*, *Xanthostemon*, *Mearnsia*, *Eucalyptopsis*, *Tristania*), and the exine is usually smooth.

The grains of *Tepualia* (monotypic) are uniformly bilateral, dicolporate, and parasyncolpate, and can be distinguished from those of all other genera in the family. The only other consistently bilateral grains (*Pileanthus*) are longicolpate and considerably larger.

Tristania neriifolia R. Br. has the smallest grains (5-7 μ) observed during the present investigation.



Figs. 39-55.—Drawings of pollen grains in polar view *A* (magnified approx. 800 diameters), and equatorial view *B* (not drawn to scale). Fig. 39.—*Metrosideros salomonensis*. Fig. 40.—*Metrosideros excelsa*. Fig. 41.—*Metrosideros parviflora*. Fig. 42.—*Spermolepis gummifera*. Fig. 43.—*Lysicarpus ternifolius*. Fig. 44.—*Cloezia buxifolia*. Fig. 45.—*Tepualia stipilaris*. Fig. 46.—*Syncarpia hillii*. Fig. 47.—*Xanthostemon crenulatus*. Fig. 48.—*Pleurocalyptus deplanchii*. Fig. 49.—*Mearnsia ramiflora* var. *humilis*. Fig. 50.—*Choricarpia leptopetala*. Fig. 51.—*Eucalyptopsis papuana*. Fig. 52.—*Tristania conferta*. Fig. 53.—*Tristania neriifolia*. Fig. 54.—*Angophora cordifolia*. Fig. 55.—*Angophora costata*.

The pollen of *Metrosideros parviflora* does not conform with that of the other species of *Metrosideros*; the grains are smaller and the colpi are absent on the polar surfaces.

The grains of *Choricarpia* are distinguished from those of *Syncarpia* by larger apocolpia and a heavier pattern.

Some species of *Xanthostemon* have parasyncolpate grains (*X. crenulatus*, *X. paradoxus*) and others syncolpate grains (*X. verdugonianus*). Similar variations are found in the species of *Tristania*.

The very small grains of *Spermolepis* (10-12 μ) are usually parasyncolpate with exceedingly small apocolpia (visible only under oil immersion).

(7) *Leptospermoideae—Leptospermeae—Eucalyptinae*

Figs. 54-60

Genera examined.—*Angophora* Cav.; *Eucalyptus* L'Herit.

Pollen grains of the two genera in this group are very similar in general features but can usually be distinguished by size differences. The grains of *Angophora* are generally larger (25-36 μ) than those of *Eucalyptus* and have a more rounded amb with slightly convex sides; they may be syn- or parasyncolpate, and often have a distinct LO-pattern which is more prominent on the lateral walls.

Grains of *Eucalyptus* species show a wide size range (10-14 μ in *E. leptophylla* to 34-36 μ in *E. miniata*); they are syn- or parasyncolpate, and in some species, e.g. *E. paniculata*, there is an apocolpium on one pole but not on the other. The exine is smooth or so lightly patterned that it appears faintly flecked. The amb usually has straight sides and rounded apices, but sometimes the sides are slightly concave or slightly convex; in *E. globulus* all three shapes have been observed in the one pollen preparation.

A thickening of the exine around the apertures is characteristic of the grains of many species of *Eucalyptus* (see Table 2). This thickening was noted by Wodehouse (1932) in grains of *E. diversicolor*, in which it gave the apertures "an almost aspidate appearance".

(8) *Leptospermoideae—Leptospermeae—Leptosperminae*

Figs. 61-69

Genera examined.—*Leptospermum* Forst.; *Agonis* DC.; *Kunzea* Reichb.; *Callistemon* R. Br.; *Melaleuca* L.; *Lamarchea* Gaud.; *Conothamnus* Lindl.

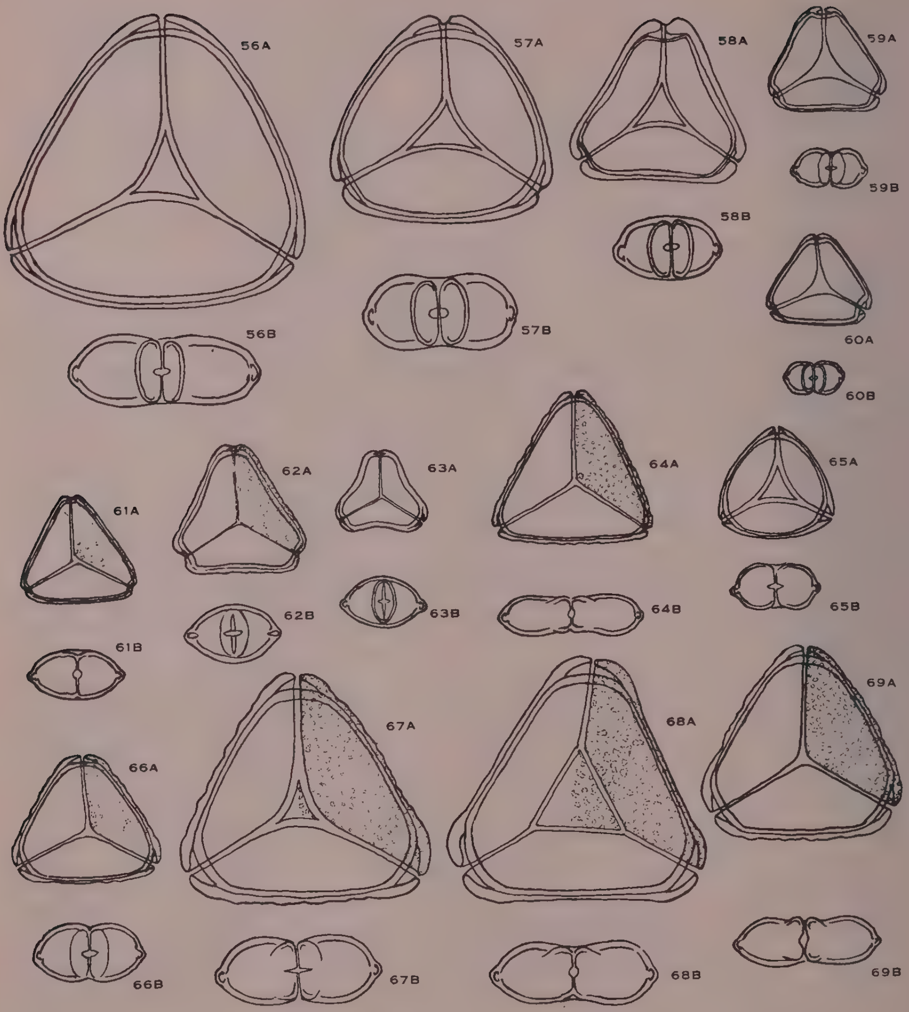
Grains of the 12 species of *Leptospermum* studied are very uniform; they are all small (10-20 μ), have a sharply triangular amb with straight or, rarely, slightly concave sides, and are syncolpate.

Couper (1953) has given a generic diagnosis for the pollen of *Leptospermum* based on a study of the grains of some New Zealand species. In his illustrations of some Recent grains polar islands are both distinct and comparatively large. In material studied during the present investigation, apocolpia have not been observed in the grains of any *Leptospermum* species.

The pollen of *Kunzea* resembles that of *Leptospermum* but can be distinguished by its slightly larger size.

The pollen of *Callistemon* has comparatively large vestibulae and apocolpia.

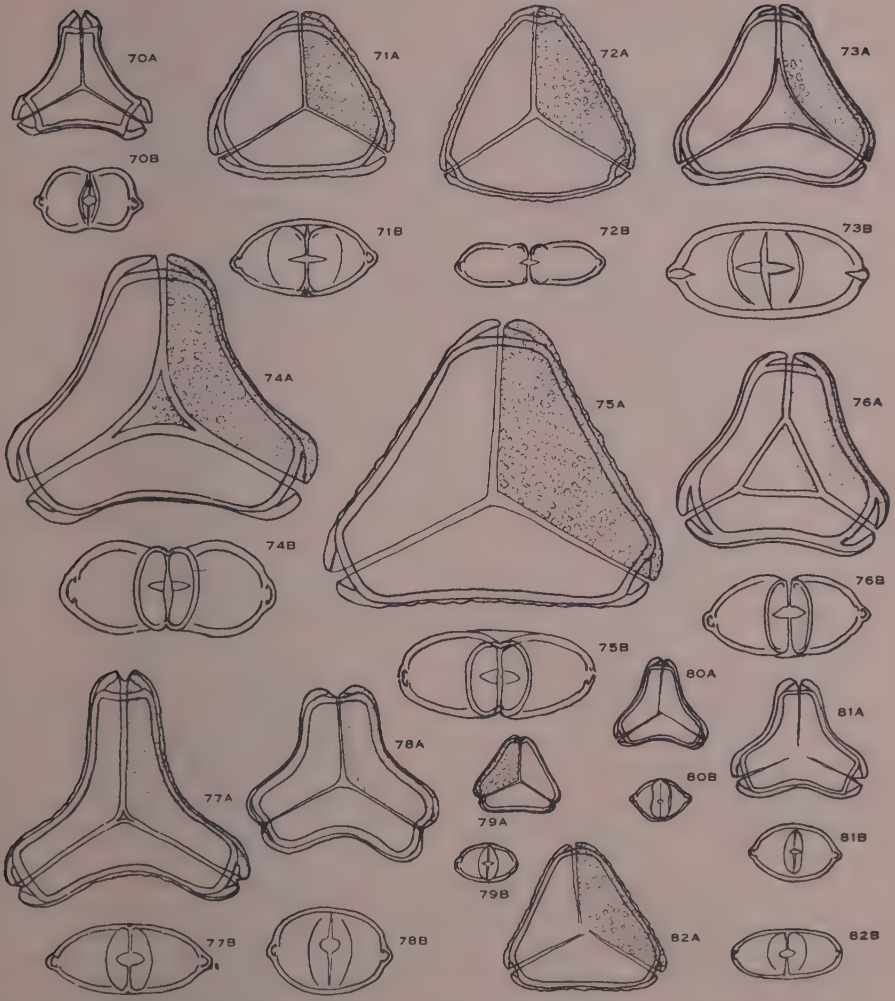
A relatively large size variation is shown by the grains of the different species of *Melaleuca*. Usually they are small (14-20 μ), syncolpate, and the pattern is very faint or absent, but the grains of *M. squamea* and *M. radula* range up to 29 μ in



Figs. 56-69.—Drawings of pollen grains in polar view *A* (magnified approx. 800 diameters), and equatorial view *B* (not drawn to scale). Fig. 56.—*Eucalyptus miniata*. Fig. 57.—*Eucalyptus globulus*. Fig. 58.—*Eucalyptus regnans*. Fig. 59.—*Eucalyptus brachyandra*. Fig. 60.—*Eucalyptus leptophylla*. Fig. 61.—*Leptospermum attenuatum*. Fig. 62.—*Leptospermum scoparium*. Fig. 63.—*Agonis marginata*. Fig. 64.—*Kunzea muelleri*. Fig. 65.—*Callistemon salignus*. Fig. 66.—*Melaleuca pauciflora*. Fig. 67.—*Melaleuca squamea*. Fig. 68.—*Lamarchea hakeaefolia*. Fig. 69.—*Conothamnus trinervis*.

equatorial diameter, although they agree in other features. The pattern, when present, is more pronounced along the lateral walls than on the polar surfaces.

The grains of *Lamarchea* are comparatively large (28-32 μ) with distinct apocolpia; in shape they resemble the larger grains of *Melaleuca*, but can be distinguished from them by their larger polar islands. Those of *Conothamnus* are faintly patterned and syncolpate.



Figs. 70-82.—Drawings of pollen grains in polar view *A* (magnified approx. 800 diameters), and equatorial view *B* (not drawn to scale). Fig. 70.—*Calothamnus torulosus*. Fig. 71.—*Eremaea ebracteata*. Fig. 72.—*Phymatocarpus porphyrocephalus*. Fig. 73.—*Regelia ciliata*. Fig. 74.—*Regelia grandiflora*. Fig. 75.—*Regelia inops*. Fig. 76.—*Beaufortia heterophylla*. Fig. 77.—*Beaufortia squarrosa*. Fig. 78.—*Balaustion pulcherrimum*. Fig. 79. *Baeckea camphorata*. Fig. 80.—*Scholtzia obovata*. Fig. 81.—*Astartea fascicularis*. Fig. 82.—*Hypocalymma robustum*.

(9) *Leptospermoideae—Leptospermeae—Calothamninae*

Figs. 70-77

Genera examined.—*Calothamnus* Labill.; *Eremaea* Lindl.; *Phymatocarpus* F. Muell.; *Regelia* Schau.; *Beaufortia* R. Br.

The pollen of *Calothamnus* is characterized by having large vestibulae. A similar feature is present in *Callistemon*, but grains of the two genera can be separated by the presence of distinct apocolpia in *Callistemon* that are absent in the syncolpate grains of *Calothamnus*.

The grains of *Eremaea* and *Phymatocarpus* are closely similar to one another, and to those of *Conothamnus*.

Pollen grains of *Regelia* show specific distinction. Those of *R. inops* are syncolpate; those of the other two species are parasyncolpate and separable on size. The grains of *R. grandiflora* are appreciably larger (31-36 μ) than those of *R. ciliata* (18-28 μ).

The pollen of the various species of *Beaufortia* also shows specific differences. Grains of *B. anisandra* and *B. heterophylla* are distinctly parasyncolpate; those of *B. decussata* and *B. sparsa* are syncolpate, or the apocolpia are exceedingly small, and those of *B. squarrosa* are subisopolar in that a small apocolpium may be present on one pole and not on the other.

(10) *Leptospermoideae—Leptospermeae—Baeckeinae*

Figs. 78-82

Genera examined.—*Balaustion* Hook.; *Baeckea* L.; *Astartea* DC.; *Scholtzia* Schau.; *Hypocalymma* Endl.

These genera differ palynologically. The extensions to the colpi are very pale or not continuous in all species examined, but there is a wide variation in size and shape.

The grains of *Balaustion* are syncolpate and prolate-spheroidal. Those of *Baeckea*, *Astartea*, and *Scholtzia* are small (8-16 μ) and almost indistinguishable from each other; they are all syncolpate and have a faint pattern, but the colpi and pattern are slightly more conspicuous in grains of *Baeckea*. Sometimes in *Astartea* and *Scholtzia* the colpi do not reach the poles. Discontinuous colpi are also characteristic of grains of *Hypocalymma*, which have a faint LO-pattern.

(11) *Leptospermoideae—Chamaelaucieae*

Figs. 83-97

Genera examined.—*Lhotzyka* Schau.; *Calythrix* Labill.; *Homalocalyx* F. Muell.; *Micromyrtus* Benth.; *Wehlia* F. Muell.; *Pileanthus* Labill.; *Chamaelaucium* Desf.; *Thryptomene* Endl.; *Actinodium* Schau.; *Darwinia* Rudge; *Homoranthus* A. Cunn.; *Verticordia* DC.

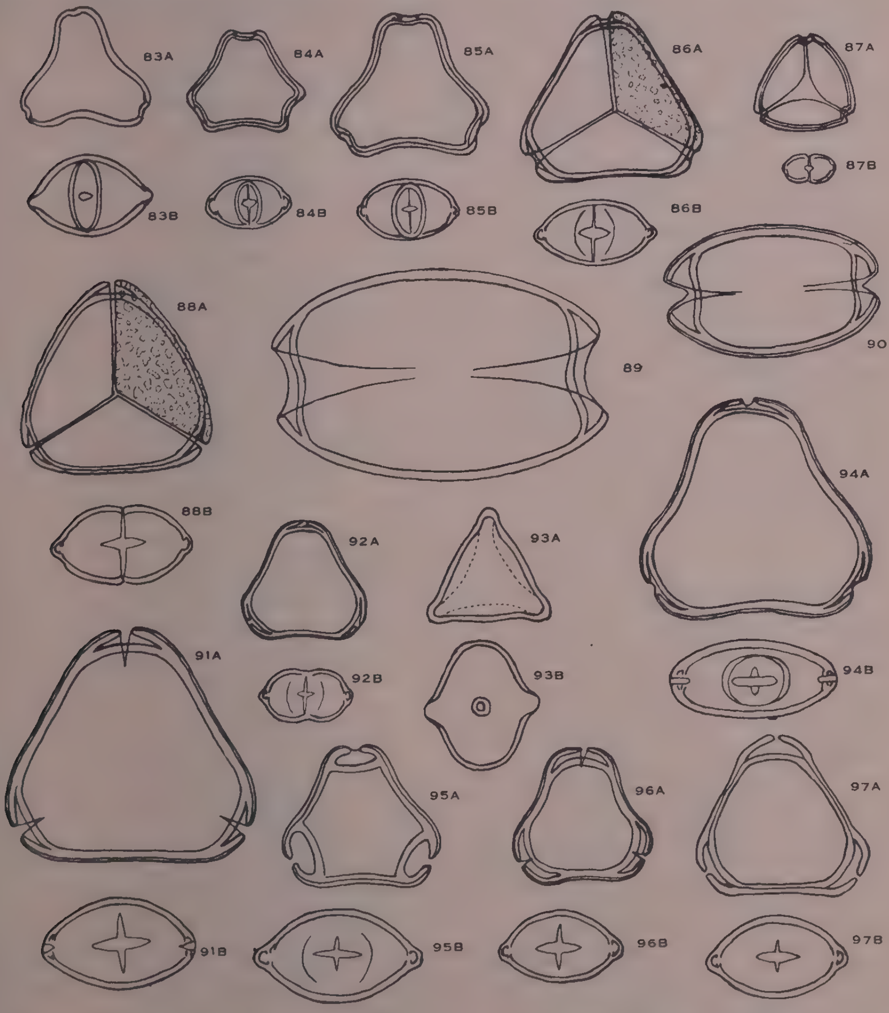
The absence of colpi on the polar surfaces, a rounded triangular amb with blunt apices and slightly concave sides, brevicolpate apertures, and a smooth exine surface are features that characterize the grains of most genera in this tribe.

Calythrix, *Chamaelaucium*, *Thryptomene*, *Darwinia*, *Homoranthus*, and *Verticordia* have grains with lalongate ora and brevissimicolpate apertures.

The pollen of *Pileanthus* (bilateral, longicolpate) and *Actinodium* (prolate-spheroidal, with ? arcoid thickenings and ? porate apertures (Erdtman 1952)) can be easily recognized and separated from that of all other genera in the family.

In size and shape the grains of *Lhotzkya* are ± close to those of *Cloezia* (Metrosiderinae) and *Agonis* (Leptosperminae).

The syncolpate, patterned grains of *Wehlia* and *Homalocalyx* are closer to those of *Hypocalymma* (Baeckeinae) than to those of other members of this group.



Figs. 83-97.—Drawings of pollen grains in polar view *A* (magnified approx. 800 diameters), and equatorial view *B* (not drawn to scale). Fig. 83.—*Lhotzkya alpestris*. Fig. 84.—*Calythrix aurea*. Fig. 85.—*Calythrix tetragona*. Fig. 86.—*Homalocalyx ericaeus*. Fig. 87.—*Micromyrtus ciliatus*. Fig. 88.—*Wehlia thryptomenioides*. Fig. 89.—*Pileanthus peduncularis*. Fig. 90.—*Pileanthus filifolius*. Fig. 91.—*Chamaelaucium uncinatum*. Fig. 92.—*Thryptomene maisonneuvii*. Fig. 93.—*Actinodium cunninghamii*. Fig. 94.—*Darwinia pauciflora*. Fig. 95.—*Darwinia diosmoides*. Fig. 96.—*Homoranthus wilhelmii*. Fig. 97.—*Verticordia densiflora*.

The one species of *Micromyrtus* studied has small, thin-walled grains with straight to slightly convex sides and very faint colpi. In these features it does not agree with those characteristic of this tribe.

VI. Discussion

Although the pollen grains of a number of genera in the Myrtaceae have previously been described, no pollen survey has been made of the family from the taxonomic point of view.

A palynological examination of genera representing all tribes of Niedenzu's classification has shown that the family has more or less uniform pollen grains, but slight differences exist which in some instances make it possible to recognize the grains of certain genera or species. Distinctive genera are: *Tepualia*, with bilateral, parasyncolpate grains that have a smooth exine (Plate 1, Fig. 11); *Pileanthus*, also with bilateral grains, but these are longicolpate and the exine surface is not quite smooth (Plate 1, Fig. 12); *Octamyrtus*, the pollen of which can be recognized by its comparatively large size (Plate 1, Fig. 1); *Actinodium*, which has small, porate, rounded grains with ? arcoid thickenings between the pores (Plate 1, Figs. 8-10). The grains of *Tristania neriifolia* are the smallest (5-7 μ) of any of the species examined; those of *Uromyrtus emarginata* are small, rounded with ± aspidate apertures; those of *Pimenta officinalis* are rounded with no extensions to the colpi and have a patterned exine; those of most members of the Chamaelaucieae are characterized by a rounded triangular amb with blunt apices, brevicolpate apertures, and a perfectly smooth exine surface.

(a) *Variation within the Family*

There appears to be no particular feature that separates pollen of the Myrtoideae from that of the Leptospermoideae, but pollen of the tribe Chamaelaucieae (placed by Niedenzu in the Leptospermoideae) differs markedly from that of all other tribes in the family.

In broad terms, three types of grains may be recognized by differences in the nature of the colpi:

(i) Longicolpate grains; These usually have a faintly patterned exine, e.g. Myrtinae, Myrciinae, and the genus *Eugenia* (sens. str.).

(ii) Syn- or parasyncolpate grains; in these the pattern is usually extremely faint or absent, e.g. Eugeniinae (excluding *Eugenia*), Backhousiinae, Metrosiderinae, Eucalyptinae, Leptosperminae, Calothamninae.

(iii) Brevi- or brevissimicolpate grains with a smooth exine surface, e.g. Chamaelaucieae (excluding *Actinodium*, *Pileanthus*, *Wehlia*, *Homalocalyx*, *Micromyrtus*).

(b) *Variation within a Tribe*

The majority of members in a single tribe usually have similar grains, e.g. Myrtinae, Chamaelaucieae, but it is possible for closely related genera to have quite distinct pollen, e.g. *Metrosideros* and *Spermolepis*, *Leptospermum* and *Agonis*, *Baeckia* and *Balaustion*, *Wehlia* and *Pileanthus*. On the other hand, grains of widely separated genera may show certain similarities, e.g. those of *Regelia ciliata* are difficult to distinguish from those of some species of *Eucalyptus*, and those of *Astartea* and *Agonis* are ± similar.

(c) *Variation within a Genus*

Grains of different species of the same genus are usually indistinguishable, e.g. *Leptospermum*, or they may be similar in general features but show a comparatively large range in size, e.g. *Melaleuca*, *Eucalyptus*. Rarely is it possible to make specific distinctions as in *Regelia*.

It is interesting to compare the generic relationships within the Myrtaceae as revealed by wood anatomy (Ingle and Dadswell 1953) with those suggested by palynology.

The diversity in the wood anatomy of the genus *Eucalyptus* is shown to less extent by the pollen. All the species of *Eucalyptus* examined have essentially the same type of grains (syn- or parasyncolpate with a rounded triangular amb and straight sides), but variable features are size, presence or absence of apocolpia and of a characteristic thickening of the exine near the apertures. Size of grain is sometimes significant in separating the pollen of some species from others. In general, size of grain diminishes when the species are arranged in the following order: bloodwoods; spotted gums; gums; stringybarks, ironbarks, peppermints, and boxes; the Mallee group. The smallest grains observed within the genus are those of *E. leptophylla* (10-14 μ), "Slender leafed white Mallee".

Ingle and Dadswell, on wood anatomical grounds, have divided the genus into two groups, A and B, *Eucalyptus* B including the "bloodwoods" and "spotted gums". In their grouping of the genera occurring in the south-west Pacific area, *Eucalyptus* B is placed with *Angophora*. They state that the timbers of *Eucalyptus* B "are very similar to those of the genus *Angophora* and anatomically it is difficult to distinguish between them." The same close connexion is shown by the pollen; in size and shape the grains of the bloodwoods and spotted gums approach those of *Angophora* species. *Eucalyptus gummifera*, *E. maculata*, *E. nowraensis*, *E. perfoliata*, *E. setosa*, and *E. terminalis* have the largest grains (27-36 μ) of the species investigated and are difficult to separate from those of *Angophora* (25-36 μ). It is of interest that the pollen of *Eucalyptus miniata*, placed by Blakely (1934) with *E. phoenicea* in the series Miniatae, is indistinguishable from that of the bloodwoods. Chattaway (1955) in her study of the anatomy of the bark of the bloodwoods has drawn attention to the close affinity of *E. miniata* with this group. Of the bloodwood species investigated, the grains of *E. tesselaris*, *E. papuana*, and *E. watsoniana*, are considerably smaller than those of *E. gummifera*, *E. perfoliata*, *E. setosa*, and *E. terminalis*.

The wood of the genus *Spermolepis* has certain anatomical features in common with *Eucalyptus* and *Angophora* and, as it appears to form a link between them, is grouped by Ingle and Dadswell with these genera. There is no palynological evidence, however, to support this relationship, as the pollen grains of *Spermolepis* are markedly different from those of *Eucalyptus* and *Angophora*, which are both of the same general type. Niedenzu placed *Spermolepis* in the Metrosiderinae, but its pollen is not in close agreement with that of any other genus in this tribe. The very small (10-12 μ), tricolporate grains of *Spermolepis* with faint colpi (parasyncolpate) appear to be closest to those of *Tristania*, but can generally be distinguished by their more rounded amb with slightly convex sides.

The genera *Acmena*, *Cleistocalyx*, *Syzygium*, and *Piliocalyx* are similar in wood anatomy and cannot be distinguished by using this character. The pollen grains of these genera, however, show slight differences. The grains of *Acmena* and *Piliocalyx* are similar to one another and can be distinguished from those of *Cleistocalyx* and *Syzygium*, which themselves cannot be separated, by their larger size, lack of apocolpia, and more rounded amb.

The separation of *Choricarpia* (formerly *Syncarpia leptopetala* F. Muell.) from *Syncarpia procera* and *Syncarpia hillii* is supported both by wood anatomy and palynology. The pollen grains of *Choricarpia* are more heavily patterned and have more pronounced apocolpia than those of *Syncarpia*, which are usually syncolpate.

The comparatively new genus *Eucalyptopsis* has certain features in common with *Pleurocalyptus*, *Syncarpia*, and *Choricarpia* of the Metrosiderinae (White 1951), and on account of these similarities has been placed in this tribe. Ingle and Dadswell (Dadswell and Ingle 1951; Ingle and Dadswell 1953) have found that in wood structure it has some similarity with the Eucalyptinae and the *Eugenia* B section of the Eugeniinae. The pollen of *Eucalyptopsis* is small and parasyncolpate, and can be distinguished from that of *Pleurocalyptus* and *Syncarpia* by its comparatively distinct apocolpia, and from that of the *Eugenia* B group by its more sharply triangular amb and faintly flecked exine. (The sharply triangular amb and small size of the grains separate them from those of the Eucalyptinae.) The closest similarity of the pollen of *Eucalyptopsis* seems to lie with that of *Tristania* and *Choricarpia*, both members of the Metrosiderinae.

Pollen of the three species of *Eugenia* A available is quite distinct from that of *Eugenia* B species. Pollen grains of the two South Africa species, *E. albanensis* and *E. capensis*, are longicolpate and have a patterned surface. In these features they resemble pollen of the Myrtinae and Myrciinae. Grains of the Australian species, *E. macrohila* (*Eugenia* A) are very much smaller but agree in being longicolpate with a faint pattern. Very limited material of *E. pronyensis*, a New Caledonian species of *Eugenia* A, has been available and the few grains seen are small, parasyncolpate (although the colpi are very faint near the poles), and patterned, and in size and shape ± resemble those of *E. stricta* (= ? *Austromyrtus stricta* Burret 1941*b*). Because of the close resemblance of this type of grain to that found in many species of *Austromyrtus*, Burret's suggested transfer of *E. stricta* to *Austromyrtus stricta* is accepted, and at the same time it is pointed out that the pollen grains of *Eugenia pronyensis* are also similar to those of *Austromyrtus* species.

The pollen grains of the two species of *Uromyrtus* investigated not only differ from one another but also from those of other members of the Myrtinae. Those of *U. artensis* resemble the pollen of a *Syzygium* or *Cleistocalyx*, while those of *U. emarginata* do not agree with other species of the family Myrtaceae. Of Burret's other new combinations (1941*a*, 1941*b*), the closely similar grains of *Rhodomyrtus* and *Pilidiostigma* are relatively large and have a rounded triangular amb. These features separate them from the smaller grains of *Austromyrtus* and *Lophomyrtus*, which are indistinguishable from one another.

The genera with pollen which appears to differ from that characteristic of the tribes in which they are placed are: *Pimenta*, *Tepualia*, *Pileanthus*, *Wehlia*, *Homalocalyx*, and *Micromyrtus*.

VII. Key to Pollen Grains of the Genera Investigated

The following provisional key is based on the species studied during the present investigation. Owing to the comparative uniformity of pollen grains of the Myrtaceae, the key primarily serves to group those genera whose grains are similar, rather than to separate individual genera.

	Grains consistently 2-aperturate	A
	Grains consistently 3-aperturate	B
A	Grains syncolpate (parasyncolpate) c. 20 μ	*Tepualia*
	Grains not syncolpate (30-40 μ)	*Pileanthus*
B	Apertures porate	*Actinodium*
	Apertures colporate	C
C	Grains syncolpate*	D
	Grains not syncolpate	L
D	Grains parasyncolpate	E
	Grains not parasyncolpate	F
E	Equatorial diameter > 25 μ	*Angophora, Eucalyptus, Lamarchea, Regelia grandiflora*
	Equatorial diameter c. 16-25 μ	*Acca, Myrrhinium, Metrosideros, Choricarpia, Callistemon, Xanthostemon, Mearnsia, Eucalyptus, Regelia ciliata, Beaufortia, Psiloxylon*
	Equatorial diameter < 16 μ	*Cleistocalyx, Syzygium, Eucalyptopsis, Tristania, Spermolepis*
F	Equatorial diameter > 20 μ	G
	Equatorial diameter < 20 μ	I
G	Grains prolate spheroidal	*Balaustion*
	Not as above	H
H	Exine surface patterned	*Eremaea, Phymatocarpus, Conothamnus, Melaleuca, Regelia inops*
	Pattern exceedingly faint or absent	*Angophora, Eucalyptus*
I	Vestibulum comparatively large, sides of amb concave	*Calothamnus*
	Not as above	J
J	Equatorial diameter between 14 and 20 μ	K
	Equatorial diameter < 14 μ	*Baeckea, Scholtzia, Cloezia, Astartea, Micromyrtus*
K	Amb triangular with straight to slightly concave sides	*Leptospermum, Kunzea, Backhousia, Syncarpia*
	Amb rounded triangular with straight to slightly convex sides	*Acmena, Piliocalyx*
L	Grains longicolpate, pattern present	M
	Grains brevicolpate, pattern faint or absent	N
M	Equatorial diameter 35-50 μ	*Octamyrtus*
	Equatorial diameter 20-35 μ	*Ugni, Calycolpus, Myrtastrum, Decaspermum, Rhodomyrtus, Fenzlia, Pilidiostigma. Eugenia* A
	Equatorial diameter < 20 μ	*Rhodamnia, Austromyrtus, Lophomyrtus, Xanthomyrtus, ? Uromyrtus, Decaspermum, Luma, Stereocaryum, Jossinia, Hypocalymma*
N	Equatorial diameter > 16 μ	*Chamaelaucium, Darwinia, Homoranthus, Verticordia*
	Equatorial diameter < 16 μ	*Lhotzkya, Calythrix*

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* If pattern distinct, more or less masking the colpi in the region of the apocolpia, turn to M.

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IX. GLOSSARY

(After Erdtman (1952))

Amb.—Outline of a pollen grain viewed with one of the poles exactly uppermost, i.e. with the polar axis directed towards the observer. (Sides of amb convex, straight, or concave.)

Angulaperturate.—The apertures are situated at the angles of the amb.

Aperture.—Any weak, preformed part of the general surface of the pollen grain which may be engaged in forming an opening in connexion with the normal exit of intra-exinous substance.

Apocolpium.—Area at a pole, delimited towards the equator by the polar limits of the mesocolpia.

Aspidate.—Grains in which the apertures (or at least their outermost parts) are borne on small ± circular areas, protruding as rounded domes from the general surface of the grains.

Bilateral.—With two vertical planes of symmetry; equatorial axes not equal.

Brevicolpate.—With ± short colpi (length of colpi equal to or shorter than total distance from colpi apices to poles).

Brevissimicolpate.—Brevicolpate grains in which the colpi are as long as or shorter than the underlying lalongate os.

Colpi (sing. *colpus*).—Equatorial, usually meridionally elongated apertures (length : breadth < 2).

Colporate.—With oriferous colpi.

Exine.—The main, outer, usually resistant layer of the wall of the pollen grain.

Isopolar.—In isopolar pollen grains there are no differences between the proximal and distal faces.

Lalongate.—Lalongate ora are transversely elongated.

*Longicolpate**.—With long colpi. Colporate grains are longicolpate when the colpi are longer than the distance between their apices and the poles.

LO-pattern.—Any pattern which at high adjustment of the microscope appears as "bright islands" separated by "dark channels", and on lower adjustment presents the reverse picture, viz. "dark islands" separated by "bright channels".

Mesocolpium.—An area delimited by two adjacent colpi and by transverse lines drawn through the apices of the colpi. The lines form the equatorial limit of the apocolpia. A mesocolpium thus borders on two colpi and two apocolpia. (In syncolpate pollen grains there are no apocolpia; in parasyncolpate grains the mesocolpia are delimited throughout by colpi.)

Nexine.—The inner, non-sculptured part of the exine.

Oblate.—The shape of a pollen grain when the ratio between polar axis and equatorial diameter is 0·75-0·50.

Ora (sing. *os*).—The inner part of a composite aperture.

Parasyncolpate.—Colpate pollen grains are parasyncolpate if the colpi (or their extensions) bifurcate, and the branches meet ± close to the poles, leaving intact apocolpia of regular shape.

Peroblate.—The shape of a pollen grain when the ratio between polar axis and equatorial diameter is $< 0\cdot50$.

Polar Areas.—The areas in radiosymmetrical pollen grains ± comparable with the polar areas of the globe.

Porate.—Pollen grains are porate when they have equatorial, ± isodiametric apertures. The limit between a porus and a colpus is defined by the length/breadth ratio of 2 : 1.

Radiosymmetric.—Radiosymmetric pollen grains have more than two vertical planes of symmetry, or, if provided with two such planes, always with equal axes.

Sexine.—The outer, sculptured part of the exine.

Stenopalynous.—Said of plant families characterized by ± slight variation in pollen types.

Subisopolar.—In subispolar pollen grains there are certain ± slight differences between the distal and the proximal face.

Subspheroidal.—The shape of a pollen grain when the ratio between the polar axis and equatorial diameter is between 0·75 and 1·33. 0·75-0·88 (suboblate); 1·00-0·88 (oblate-spheroidal); 1·14-1·00 (prolate-spheroidal); 1·14-1·33 (subprolate).

Syncolpate.—With colpi anastomosing at the poles.

Vestibulum†.—Cavity forming the pore and being separated from the interior of the grain by a low rim or by separation between different layers of the exine.

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* Not defined by Erdtman (1952).

† Faegri and Iverson (1950).

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EXPLANATION OF PLATE 1

All the photographs are from untouched negatives. The figures are of acetolysed pollen grains, magnified 1000 times.

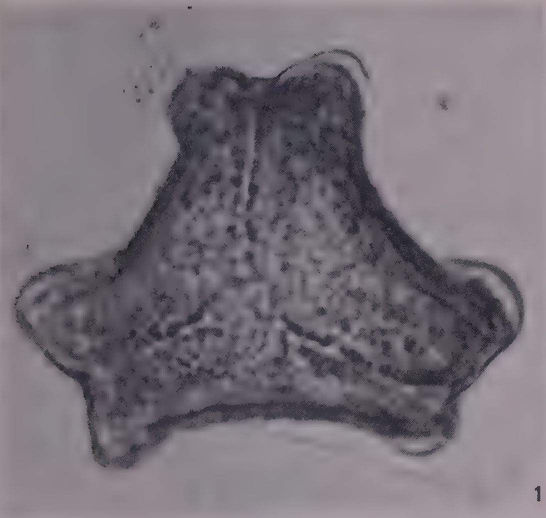
Fig. 1.—*Octamyrtus behrmannii* (longicolpate).

Fig. 2.—*Eucalyptus setosa*; equatorial view.

Fig. 3.—*Rhodomyrtus trineura* (LO-pattern).

Fig. 4.—*Eucalyptus miniata* (parasyncolpate).

POLLEN MORPHOLOGY OF MYRTACEAE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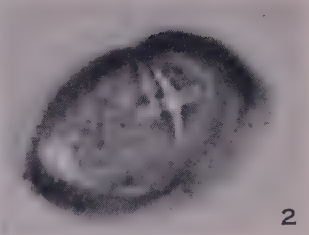
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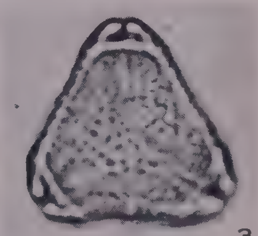
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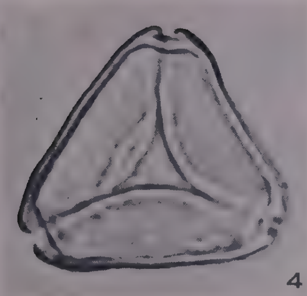
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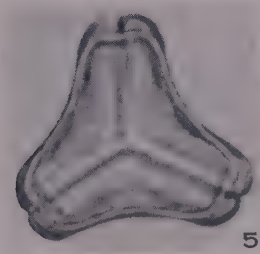
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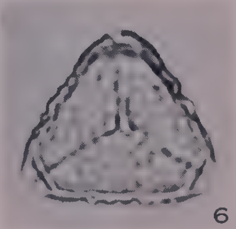
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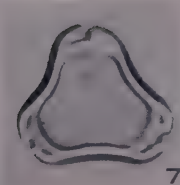
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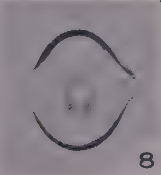
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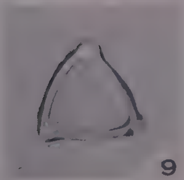
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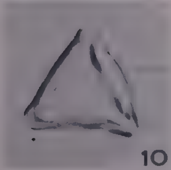
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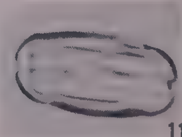
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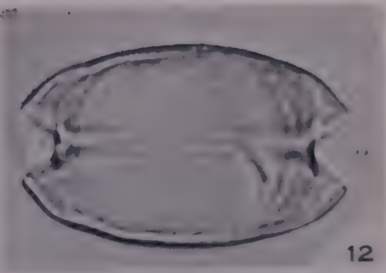
12

MONOLETE, MONOCOLPATE, AND ALETE SPOROMORPHS FROM AUSTRALIAN PERMIAN SEDIMENTS

By B. E. Balme* and J. P. F. Hennelly*

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Summary

Isolated monolete, monocolpate, and alete sporomorphs have been found to occur frequently in Australian coals and shales of Permian age. The structure, distribution, and possible affinities of a number of the more common types have been discussed and an attempt made to classify the sporomorphs described on the basis of their germinal mechanism and ornament.

Seven new sporomorphs and one new form have been assigned to one or other of the existing sporotypes, *Laevigatosporites* Ibrahim, *Tuberculatosporites* Imgrund, *Verrucososporites* (Knox) Potonié & Kremp, and *Entylissa* (Naumova) Potonié & Kremp. *Marsupipollenites* n. spt. and *Pilasporites* n. spt. have been instituted as new sporotypes.

I. Introduction

During recent investigations into the stratigraphical palynology of Australian Upper Palaeozoic coal deposits, large numbers of morphologically diverse spores and pollen grains have been isolated from coals and other carbonaceous sediments of Permian age. Some of these have already been described (Balme and Hennelly 1955), and this account deals with three further morphological groups of sporomorphs: monolete spores with a longitudinal tetrad scar, sporomorphs with a single distal furrow, and a rather nondescript group of forms without a clearly defined dehiscence mechanism.

The classification used in this account is in principle that proposed by Potonié and Kremp (1954).

II. Monolete Sporomorphs

All sporomorphs with a single, more or less straight proximal tetral scar which serves also as a germinal exit have been placed under the division Monoletes (Ibrahim) Potonié & Kremp by the emending authors. When dealing with isolated fossil sporomorphs it is of course frequently impossible to differentiate between spores *sensu stricto* and pollen grains; so that recourse must be taken to morphological analogies of uncertain validity. From Seward's (1919, p. 425) illustrations for example, the pollen grains of the coniferalean fructifications *Masculostrobus zeilleri* Seward and *Masculostrobus* sp. would be necessarily classified under Monoletes if encountered as independent microfossils in sediments. However, after making allowance for doubtful or distorted forms, the majority of isolated Palaeozoic monolete sporomorphs previously described, so closely resemble the spores of modern bryophytes and pteridophytes that their origin from members of these divisions may be accepted.

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Apart from this generalization, the production of bilateral monolete spores is an unreliable guide to plant affinities. They are found today among the Musci (Knox 1939), Psilotales (Knox 1938; Selling 1946), Isoëtaceae (Knox 1950), and particularly among the Filicales (e.g. Selling 1946; Knox 1951). Knox's (1950, p. 336) suggestion that isolated Palaeozoic, bilateral spores are predominantly of filicalean affinity, while reasonable at least in the case of heavily sculptured forms, is unsupported by direct evidence. Monolete spores are, in fact, remarkably rare in fossil fructifications, although Reed (1938) has reported them in a calamarian cone from the Carboniferous of Illinois.

The most ancient occurrence of free bilateral spores recorded appears to be in coals from the base of the Fell Sandstone, Northumberland (Raistrick 1938) which lies in the Main Seminula Zone of the Upper Avonian. There is no doubt, however, that they are most uncommon elsewhere in the Lower Carboniferous of the northern hemisphere. Knox (1948) did not observe monolete types in the Scottish Limestone coals, and Butterworth and Millott (1955) found them to be absent in coals below the base of the Middle Coal Measures in North Staffordshire. Naumova (1937) states that they appear first in Upper Carboniferous coals in Russia, and in Illinois Kosanke (1950) did not record the monolete sporotype *Laevigatosporites* Ibrahim below the Reynoldsburg coal (Namurian C.). Monolete sporomorphs corresponding to one or other of the forms of *Laevigatosporites vulgaris* Ibrahim are extremely abundant in many northern hemisphere, Upper Carboniferous coal seams, but few other types have been recorded. However, in the Stephanian and Lower Permian coals of the Kaiping basin in China, Imgrund (1952) found a considerable variety of monolete types: a multiplicity which is said to be matched in the Rotliegendes in Germany (Potonié and Kremp 1954, p. 164).

Earlier studies of Australian Permian sporomorphs (e.g. Dulhunty 1945; de Jersey 1946; Balme 1952) have indicated that bilateral, monolete forms are common in many coals, although it should be noted that in none of the papers cited was an attempt made to distinguish between monolete spores and monocolpate pollen grains. In the coals of Indian Gondwanaland similar sporomorphs appear to be rarer. Virkki (1945, Plate 3, Fig. 34) figured only one clearly monolete spore and few additional bilateral types have been described by more recent Indian authors (e.g. Ghosh and Sen 1948; Sen 1953; Surange, Srivastava, and Prem Singh 1953).

III. Descriptions of Monolete Sporomorphs

Laevigatosporites (Ibrahim), Schopf, Wilson, & Bentall

Laevigatosporites **Ibrahim, 1933.**

Laevigatosporites (Ibrahim), Schopf, Wilson, and Bentall, 1944, p. 36.

Laevigatosporites vulgaris **Ibrahim, 1933.**

Laevigatosporites vulgaris forma *colliensis* forma nov.

Plate 1, Figs. 1-5.

Synonymy

P3E Balme 1952.

Type Locality.—Main seam, Proprietary Colliery, Collie, W.A.

Dimensions (20 specimens).—Longitudinal axis 50-76 μ (mean 61 μ), transverse axis 31-51 μ (mean 41 μ).

Amb oval. Proximal suture clearly defined, usually closed, occasionally open (Plate 1, Fig. 1) forming a fusiform rent in the proximal face. Exine thin, unornamented, susceptible to folding and tearing during compression so that many isolated specimens are distorted.

Discussion.—Common in the coals of Collie, but not observed in any Australian Permian sediments outside Western Australia. Virkki's spore 10 (Virkki 1945, Plate 3, Fig. 34) is morphologically similar.

Occurrence

WESTERN AUSTRALIA: Collie (all seams); Irwin River; Wilga; Eradu.

Laevigatosporites scissus n. spm.

Plate 1, Figs. 6-9

Type Locality.—Greta seam, Hebburn No. 2 Colliery, N.S.W.

Dimensions (30 specimens).—Longitudinal axis 19-34 μ (mean 26 μ), transverse axis 16-27 μ (mean 20 μ).

Amb oval. In most specimens the longitudinal monolete dehiscence line extends the full length of the proximal face and on to the distal surface. The expanded sporomorph tends, therefore, to split into two equal parts. Exine thin, unornamented or faintly granulate.

Discussion.—The morphology of this sporomorph is unusual and its assignation to *Laevigatosporites* must be regarded as tentative.

Occurrence

NEW SOUTH WALES: Greta Stage; Tomago Stage; Newcastle Stage.

TASMANIA: Illamatha; Tarleton.

WESTERN AUSTRALIA: Collie; Irwin River; Eradu.

Tuberculatosporites Imgrund

Tuberculatosporites Imgrund, 1952, p. 65.

Tuberculatosporites modicus n. spm.

Plate 1, Figs. 10-13

Synonymy

P28B Balme 1952.

Type Locality.—Main seam, Westralia Colliery, Collie, W.A.

Dimensions (20 specimens).—Longitudinal axis 18-30 μ (mean 25 μ), transverse axis 10-25 μ (mean 18 μ).

Amb oval. Monolete scar extending full length of proximal face, closed, or delineated by a longitudinal fold in the exine. Exine about 1 μ thick ornamented with short, stout spines about 1·5 μ long and 1 μ in basal diameter.

Occurrence

WESTERN AUSTRALIA: Collie; Irwin River; Eradu.

Verrucososporites (Knox) Potonié & Kremp

Verrucososporites Knox, 1950, p. 316.

Verrucososporites (Knox) Potonié & Kremp, 1954, p. 166.

Verrucososporites cicatricosus n. spm.

Plate 1, Figs. 14-18

Type Locality.—Greta seam, Hebburn No. 2 Colliery, N.S.W.

Dimensions (18 specimens).—Longitudinal axis 34-42 μ (mean 38 μ), transverse axis 23-34 μ (mean 28 μ).

Amb oval. Proximal side flattened and distal rounded, in laterally compressed specimens. Monolete suture extending almost full length of proximal face. Exine considerably thickened (about 5 μ) on distal surface which is ornamented with heavy irregular ridges about 5 μ wide. Ornament reduced or absent on proximal face.

Discussion.—The structure and ornament of *V. cicatricosus* resembles that found in the spores of certain modern members of the Polypodiaceae, and similar sporomorphs from Mesozoic deposits have been described under the sporotype *Polypodiidites* Ross (Ross 1949; Couper 1953).

Occurrence

NEW SOUTH WALES: Greta and Homeville seams.

Verrucososporites hamatus n. spm.

Plate 1, Figs. 19-21

Type Locality.—Coal band at 248 ft 7 in., Dobbs Drift, State Mine, Lithgow, N.S.W.

Dimensions (16 specimens).—Longitudinal axis 45-52 μ (mean 49 μ), transverse axis 30-41 μ (mean 37 μ).

Amb oval. Proximal face flattened and distal rounded in lateral view. Monolete scar extending full length of proximal face, lips sometimes slightly out-turned. Exine thickened on distal side, ornamented with spinose, hooked, or truncated protuberances 3-6 μ long and about 3 μ basal diameter. Proximal side originally wedge shaped, either smooth or with reduced ornament.

Occurrence

NEW SOUTH WALES: Newcastle and Tomago Stages.

Verrucososporites leopardus n. spm.

Plate 1, Figs. 22-24

Probable synonymy

P28A Dulhunty 1945.

P28A (Dulh.) Dulhunty and Dulhunty 1949.

Type Locality.—Homeville seam, Hebburn No. 1 Colliery, N.S.W.

Dimensions (25 specimens).—Longitudinal axis 40-54 μ (mean 46 μ), transverse axis 24-44 μ (mean 35 μ).

Amb oval or subcircular. Monolete scar marked by a longitudinal fold in the exine extending the full length of proximal face. Sexine ornamented with closely packed, flattened verrucae 1-2 μ in diameter, about 0·5 μ high and less than 1 μ apart.

Occurrence

NEW SOUTH WALES: Greta and Homeville seams.

TASMANIA: Illamatha; Tarleton.

IV. MONOCOLPATE SPOROMORPHS

Pollen grains possessing a single longitudinal germinal furrow on the distal face have been regarded by Wodehouse (1935, p. 236) as the most primitive of all pollens, and hence as the likely evolutionary progenitors of more elaborate modern types. They are today widespread among the gymnosperms, particularly the Cycadales, and occur also among a number of angiosperm families. Certain members of two extinct plant groups, the Bennettitales and Pteridospermae are also known to have produced single-furrowed pollen grains. Except for the occasional development of prothallial tissue the known pollen of the Bennettitales (Wieland 1906; Nathorst 1909) closely resembles that of modern and extinct cycads. Such tissue would, however, not be expected to survive any form of preservation other than petrification, so that no criteria exist for separating the isolated pollen grains of the Bennettitales and Cycadales. The single-furrowed pollen grains of certain Upper Palaeozoic pteridosperms are, on the other hand, quite characteristic and of possible taxonomic significance.

Apart from that of a few genera (e.g. *Urnatopteris*, *Renaultia*), which produced pollen grains resembling trilete fern spores, the known pollen of Palaeozoic pteridosperms falls into two main morphological categories:

(*a*) Prolate grains 100-500 μ in length, possessing two broad longitudinal folds on the distal surface and a monolete tetrad scar on the proximal face.

(*b*) Smaller spheroidal or prolate grains, possessing a distal furrow and in some species a proximal trilete or monolete tetrad scar.

The first type of pollen is known to have been produced by fructifications of the *Whittleseya* and *Dolerotheca* types (cf. Halle 1933; Florin 1937; Schopf 1948) which are considered to have been borne by certain species of *Neuropteris*, *Alethopteris*, *Lonchopteris*, and *Odontopteris* (Remy 1954), in turn related to the anatomical group Medulloseae. Pollen grains of a similar type occur as independent microfossils in many northern hemisphere Upper Carboniferous coals. They were first described by Ibrahim (1932) from the Westphalian of the Ruhr and have been frequently reported by subsequent authors in both Europe and North America (e.g. Schopf 1938; Dijkstra 1946). According to Dijkstra they range from the Westphalian A in the Netherlands to the Westphalian D of the Saar basin. No sporomorphs of the

Whittleseya-Dolerotheca type have been recorded from Palaeozoic deposits in the southern hemisphere.

Smaller single-furrowed pollen grains of the second type were produced by a number of different groups of pteridosperm fructifications. Their morphology was first interpreted by Halle (1933) when studying the pollen of *Potoniea carpentieri* (Kidst.) Halle, and further investigations by Florin (1937) have shown that other species of *Potoniea* produced similar pollen grains. Some species of *Telangium*, *Psilangium*, and *Schuetzia* (Florin 1937; Remy 1954) have single-furrowed pollen grains which, like those of *Potoniea carpentieri*, also possess a trilete tetrad scar on the proximal face. The pollen grains of *Zeilleria* are equipped with a distal furrow but here the proximal tetrad marking is monolete. Florin (1937, p. 329) considered that most of the fructifications containing these small monocolpate pollens were borne on fronds of the *Sphenopteris* type, but others are known to be derived from *Linopteris*, *Pecopteris*, *Rhodea*, *Paripteris*, and *Reticulopteris* (Remy 1954). In view of the great abundance of fronds belonging to these form genera in shales of the Upper Carboniferous coal measures in Europe, it is perhaps surprising that no sporomorphs resembling the small monocolpate pollens of pteridosperms have been recorded from the associated coals.

Small oval or fusiform sporomorphs with a single germinal furrow, conforming to the Ginkgoales-Bennettitales-Cycadales pollen type, appear first in Upper Palaeozoic sediments and are frequently encountered in these and younger deposits in both the northern and southern hemisphere. Naumova recorded them from Lower Permian Siberian coals, while they were found by Luber (1938) to form an important part of the sporomorph flora of the Upper Permian coals of the Kuznetsk basin. They appear to increase in abundance in the European Mesozoic (Nathorst 1908; Thiergart 1949), and in Australia they have been reported by de Jersey (1949) from Queensland Triassic coals and by Edwards, Baker, and Knight (1944) from the Jurassic coals of Wonthaggi, Vic. Except possibly for one spore figured by Virkki (1945, Plate 3, Fig. 35), there is no record of this type of sporomorph from the Gondwanaland coals of India.

V. Classification of Monocolpate Sporomorphs

Isolated large pollens of the *Whittleseya-Dolerotheca* type were originally classified by Ibrahim (1932) under the general group name *Sporonites* and later transferred (Ibrahim 1933) to the sporotype *Laevigatosporites*. They have received varying taxonomic treatment from other authors. Loose (1934) placed them in *Punctatosporites*. Wicher (1934) under a group designation *Sporites*, while Schopf (1935, 1938) reduced Ibrahim's term *Monoletes* to the status of a sporotype to include isolated sporomorphs with the characteristics of *Whittleseya* pollen. Recently Potonié and Kremp have created the sporotype *Schopfipollenites* for these sporomorphs, placing it in a separate division, Precolpates. The term Precolpates apparently implies that the sporomorphs are prepollen in the sense of Renault and Schopf; that is either that they produced prothallial tissue or that the germinal exit was proximal. It is unlikely that either of these criteria can be adequately demonstrated when considering isolated pollen grains, and the distinction made by Potonié and Kremp, between precolpate and monocolpate Palaeozoic pollen grains is difficult to maintain.

Monocolpate pollen grains of the Bennettitalian-Cycadalean type were classified by Naumova (1937) under the sporotype *Entylissa* although she described no individual sporomorphs. Potonié and Kremp (1954, p. 181) have therefore regarded *Entylissa* (*Azonaletes*) *caperatus* Luber (1938) as the type, in their emendation of *Entylissa* as a sporotype under the division Monocolpates.

VI. Descriptions of Monocolpate Sporomorphs

Marsupipollenites n. spt.

The name *Marsupipollenites* is proposed for isolated sporomorphs having the following characteristics:

Maximum diameter under 150 μ. Amb oval or circular. Single furrow on the distal face delimited by two longitudinal folds in the exine. These folds may be in contact or overlapping at the distal pole in unexpanded sporomorphs. In ruptured grains an irregular rent occurs in the distal face, bordered by a narrow zone of folded exine (Plate 2, Figs. 34-35). A trilete or monolete tetrad scar may be present on the proximal face. Sexine ornament rugose, granulate, verrucate, or striate.

Discussion.—Sporomorphs classified under *Marsupipollenites* are morphologically similar to the pollen grains of certain Palaeozoic pteridosperms, particularly those of *Potoniea* and *Psilangium*, although no suggestion is made that they necessarily arise from these or even closely related plants. Certain of the striate forms of *Marsupipollenites* are reminiscent of the bisaccate sporomorphs of *Lueckisporites*, and possibly represent members of the latter group in which bladder development has been arrested. Tchigouriaeva (1949) has previously suggested that a series of Palaeozoic transversely striated sporomorphs exists, including both bisaccate and non-bladdered forms.

Marsupipollenites triradiatus n. spm. is designated as the genotype.

Marsupipollenites triradiatus n. spm.

Plate 2, Figs. 29-35

Synonymy

P8A Dulhunty 1945 (in part).

P8A (Dulh.) de Jersey 1946 (in part).

P8A (Dulh.) Balme 1952.

P9C Balme 1952.

Type Locality.—Seam at 688 ft, South Wallarah No. 5 bore, N.S.W. (Newcastle Stage).

Dimensions (70 specimens).—Longitudinal axis 42-73 μ (mean 55 μ), transverse axis 25-65 μ (mean 42 μ).

Amb of unexpanded grain oval. Distal furrow bordered by two longitudinal overfolds in exine extending full length of the grain. Small trilete tetrad scar on proximal face, rays of scar about 6 μ long, sometimes open forming a triangular rent in the exine at the proximal pole. Expanded grain (Plate 2, Fig. 35) subcircular, distal side ruptured, rupture bordered by a narrow zone of folded exine. Exine about 2 μ thick on proximal face ornamented with flattened verrucae, granules, or fine indeterminate markings.

Discussion.—Very abundant in most Australian Permian carbonaceous deposits. In New South Wales it is particularly common in coals from the Newcastle Stage.

Occurrence

NEW SOUTH WALES: Greta, Tomago, and Newcastle Stages.

TASMANIA: Illamatha; Tarleton. P8A (Dulh.) also recorded from the Upper Coal Measures (Dulhunty and Dulhunty 1949).

WESTERN AUSTRALIA: Collie (particularly in the Collie Burn and Cardiff coals); Irwin River; Eradu.

Marsupipollenites triradiatus forma *striatus* forma nov.

Plate 2, Figs. 36-37

Type Locality.—Lithgow seam, Kandos Colliery, N.S.W.

Dimensions (9 specimens).—Longitudinal axis 45-75 μ (mean 59 μ), transverse axis 40-65 μ (mean 49 μ).

Amb of unexpanded grain oval. Distal furrow bordered by longitudinal marginal folds. Small trilete tetrad scar or triangular opening at proximal pole. Exine about 2 μ thick on proximal side, ornamented by parallel or curved transverse thickenings 1-5 μ in width.

Occurrence

NEW SOUTH WALES: Newcastle Stage.

WESTERN AUSTRALIA: Collie; Eradu.

Marsupipollenites sinuosus n. spm.

Plate 2, Figs. 25-28

Synonymy

P3B Dulhunty 1945.

P3B (Dulh.) Dulhunty and Dulhunty 1949.

P3B (Dulh.) Balme 1952.

Type Locality.—Seam at 688 ft South Wallarah No. 5 bore, N.S.W. (Newcastle Stage).

Dimensions (20 specimens).—Longitudinal axis 70-101 μ (mean 85 μ), transverse axis 32-48 μ (mean 39 μ).

Amb oval or fusiform. Proximal side slightly flattened in lateral view. Distal furrow bordered by two longitudinal, slightly crescentic folds extending almost the full length of the grain and in contact at their extremities. Distal folds usually turned outwards at their inner margins, giving rise to subsidiary longitudinal folds so that the sporomorph has a characteristic wrinkled appearance. Monolete tetrad scar on proximal face with a slight angular deflection at the proximal pole. Exine about 2 μ thick, smooth or faintly granulate.

Discussion.—In structure *M. sinuosus* resembles the pollen of *Whittleseya* and *Dolerotheca* although it is smaller than that of any known species of these genera. For this reason it has not been placed under the sporotype *Schopfipollenites.*

Occurrence

NEW SOUTH WALES: Tomago and Newcastle Stages; Muswellbrook coal.

TASMANIA: P3B has been reported from both Upper and Lower Coal Measure seams (Dulhunty and Dulhunty 1949).

WESTERN AUSTRALIA: Collie (Cardiff seam).

Marsupipollenites scutatus n. spm.

Plate 2, Figs. 38-41

Type Locality.—Homeville seam, Hebburn No. 1 Colliery, N.S.W.

Dimensions (25 specimens).—Longitudinal axis 43-52 μ (mean 46 μ), transverse axis 34-58 μ (mean 48 μ).

Amb circular or oval. Plano-convex, distal side flattened, in lateral view. Distal folds sometimes overlapping at the distal pole. Exine fairly thick, reaching 4 μ at the free margins of the distal folds. Sexine ornamented on the proximal side by transverse striate thickenings 1-3 μ wide and about 0·5 μ apart. On the distal side the striae break up into flattened verrucae 1-3 μ in diameter and less than 1 μ high.

Occurrence

NEW SOUTH WALES: Greta and Homeville seams.

TASMANIA: Tarleton.

WESTERN AUSTRALIA: Collie, Main seam (very rare).

Marsupipollenites fasciolatus n. spm.

Plate 3, Figs. 42-45

Synonymy

P23C Balme 1952.

Type Locality.—Main seam, Co-operative Colliery, Collie, W.A.

Dimensions (20 specimens).—Longitudinal axis 25-38 μ (mean 34 μ), transverse axis 30-46 μ (mean 39 μ).

Amb oval, elongated transversely. Distal furrow 8-15 μ wide, marginal folds narrow and irregularly developed. Sexine ornamented with about 15 transverse striate thickenings 2-4 μ wide and less than 1 μ apart. In some specimens the striae continue on to the distal face but in others they are confined to the proximal area. In some torn specimens (Plate 3, Figs. 42-43) a thin finely punctate nexine is exposed.

Occurrence

WESTERN AUSTRALIA: Collie.

NEW SOUTH WALES: Similar but probably not identical forms have been occasionally observed in maceration residues from Newcastle Stage coals.

Entylissa (Naumova) Potonié & Kremp

Entylissa Naumova 1937, p. 355.

Entylissa (Naum.) Potonié and Kremp, 1954, p. 181.

Entylissa vetus n. spm.

Plate 3, Figs. 49-52

Probable synonymy

P3A Dulhunty 1945.

Type Locality.—Homeville seam, Lower Split, Hebburn No. 1 Colliery, N.S.W.

Dimensions (20 specimens).—Longitudinal axis 30-48 μ (mean 37 μ), transverse axis 18-36 μ (mean 26 μ).

Amb oval. Distal furrow extending full length of grain, slightly expanded at extremities. Exine 1-3 μ thick, smooth or faintly granulate.

Occurrence

NEW SOUTH WALES: Greta Stage; Tomago Stage; Newcastle Stage.

TASMANIA: Illamatha; Tarleton.

Entylissa cymbatus n. spm.

Plate 3, Figs. 53-56

Type Locality.—Homeville seam, Lower Split, Hebburn No. 1 Colliery, N.S.W.

Dimensions (15 specimens).—Longitudinal axis 42-54 μ (mean 49 μ), transverse axis 18-29 μ (mean 24 μ).

Amb elongated oval. Distal furrow extends full length of grain, when closed slightly expanded at extremities (Plate 3, Figs. 53-55). Exine thin, granulate.

Occurrence

NEW SOUTH WALES: Greta and Homeville seams.

VII. ALETE SPOROMORPHS

Sporomorphs without clearly defined germinal apparatus have been recorded from sediments of all geological ages from the Carboniferous onwards. Little attention has been paid to them by palynologists, although Ibrahim (1933) recorded alete spores from the Ruhr coals and both Naumova (1937) and Luber (1938) found them in Russian Permian deposits. Potonié and Kremp regard Erdtmann's group name Napites as a division in their classification of Palaeozoic sporomorphs but they list no sporotypes under it. They do, however, imply that alete sporomorphs are generally pollen grains in the strict sense. However, although alete grains are common enough among present-day gymnosperms and angiosperms, spores of similar morphology also occur among the Pteridophyta (e.g. *Equisetum arvense*) and Bryophyta (Knox 1939). Very little can therefore, be inferred as to the relationships of isolated Palaeozoic alete sporomorphs. It is obvious also that, in the absence of germinal apparatus, few criteria exist by which such sporomorphs may be readily differentiated for stratigraphical purposes. The sporomorphs described here are therefore to be regarded only as general form categories, each of which may include the spores and pollen grains of many unrelated plants.

Pilasporites n. spt.

The sporotype *Pilasporites* is proposed for sporomorphs of unknown affinities having the following characteristics:

Compressed spore body circular, subcircular, or oval. Germinal and tetrad markings absent although exine may be irregularly ruptured. Sexine smooth, granulate, or microreticulate.

Pilasporites calculus n. spm. is designated as the genotype.

Pilasporites calculus n. spm.

Plate 3, Figs. 60-64

Type Locality.—Greta seam, Hebburn No. 2 Colliery, N.S.W.

Dimensions (30 specimens).—Longitudinal axis 45-75 μ (mean 55 μ), transverse axis 28-60 μ (mean 43 μ).

Subcircular in usual planes of compression. No marked germinal mechanism although an irregular or oval rupture occurs in many specimens (Plate 3, Figs. 62-63). Exine differentially thickened, reaching 8 μ on the face opposite the rupture in some specimens. Sexine smooth, granulate, or finely reticulate.

Occurrence

NEW SOUTH WALES: Greta Stage.

TASMANIA: Illamatha; Tarleton.

Pilasporites plurigenus n. spm.

Plate 3, Figs. 57-59

Probable synonymy

P5C Dulhunty 1945.

P5C (Dulh.) de Jersey 1946.

P5C (Dulh.) Dulhunty and Dulhunty 1949.

P5D Balme 1952.

Type Locality.—Greta seam, Hebburn No. 2 Colliery, N.S.W.

Dimensions (40 specimens).—Diameter 12-36 μ (mean 20 μ).

Circular or subcircular. No germinal mechanism visible in intact specimens but irregular rupture of the exine common. Exine 2-4 μ thick, smooth or faintly granulate.

Discussion.—A very common form in almost all Australian Permian coals.

Incertae sedis

Sporomorph "A"

Plate 3, Figs. 66-67

Type Locality.—Greta seam, Hebburn No. 2 Colliery, N.S.W.

Dimensions (20 specimens).—Diameter 45-64 μ (mean 53 μ).

Subcircular to quadrilateral in usual planes of compression. No clear germinal mechanism, although a small notch or rupture is usually visible at the middle of one margin of the flattened sporomorph. Exine 1-2 μ thick, smooth or with widely separated irregularly disposed verrucae.

Discussion.—The morphology of this sporomorph is uncertain but it has been illustrated because of its possible stratigraphic importance. Up to the present it has been observed only in coals from the Greta Stage of New South Wales and the Lower Permian coal measures of Tasmania.

Occurrence

NEW SOUTH WALES: Greta, Homeville, and Muswellbrook seams.

TASMANIA: Illamatha; Tarleton.

VIII. ACKNOWLEDGMENTS

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EXPLANATION OF PLATES 1-3

All magnifications × 500.

PLATE 1

Fig. 1.—*Laevigatosporites vulgaris* forma *colliensis* forma nov. Proximal view, monolete scar open.
Fig. 2.—*L. vulgaris* f. *colliensis* f. nov. Proximal view, folded specimen.
Figs. 3-5.—*L. vulgaris* f. *colliensis* f. nov.
Figs. 6-9.—*Laevigatosporites scissus.* n. spm.
Figs. 10-13.—*Tuberculatosporites modicus* n. spm.
Fig. 14.—*Verrucososporites cicatricosus* n. spm. Proximal view.
Fig. 15.—*V. cicatricosus* n. spm. Distal view.
Figs. 16-17.—*V. cicatricosus* n. spm. Lateral view.
Fig. 18.—*V. cicatricosus* n. spm. Proximal view.
Fig. 19.—*Verrucososporites hamatus* n. spm.
Fig. 20.—*V. hamatus* n. spm. Semilateral view.
Fig. 21.—*V. hamatus* n. spm. Lateral view.
Figs. 22-24.—*Verrucososporites leopardus* n. spm. Proximal view.

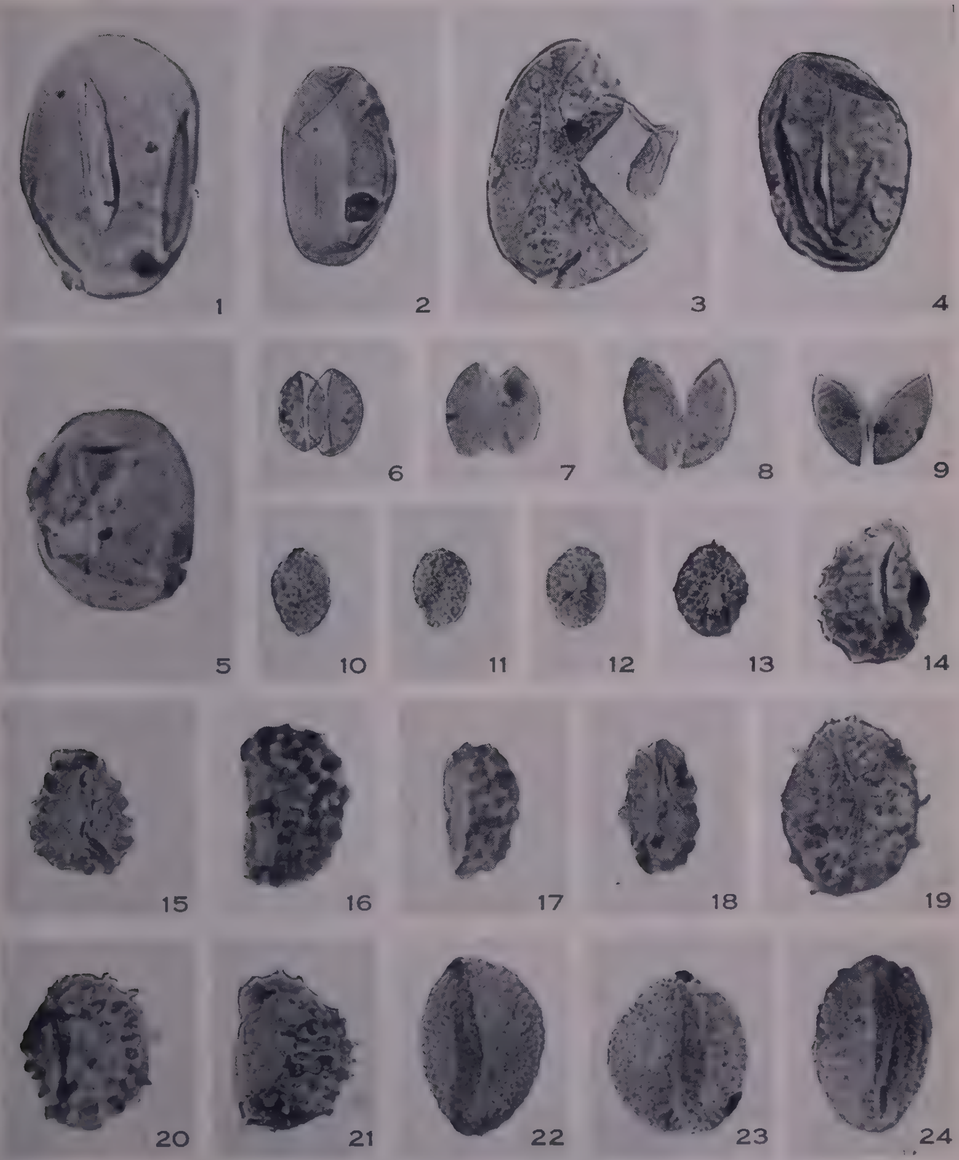
PLATE 2

Figs. 25-28.—*Marsupipollenites sinuosus* n. spm. Distal view.
Figs. 29-30.—*Marsupipollenites triradiatus* n. spm. Unexpanded grain, distal view.
Fig. 31.—*M. triradiatus* n. spm. Unexpanded grain, distal folds slightly turned back at inner margins.
Fig. 32.—*M. triradiatus* n. spm. Semilateral view.
Fig. 33.—*M. triradiatus* n. spm. Unexpanded grain. Distal folds in contact at distal pole.
Figs. 34-35.—*M. triradiatus* n. spm. Expanded grains.
Fig. 36.—*Marsupipollenites triradiatus* forma *striatus* forma nov. Expanded grain.
Fig. 37.—*M. triradiatus* f. *striatus* f. nov. Unexpanded grain.
Figs. 38-39.—*Marsupipollenites scutatus* n. spm. Unexpanded grains, distal view.
Figs. 40-41.—*M. scutatus* n. spm. Expanded grains.

PLATE 3

Figs. 42-43.—*Marsupipollenites fasciolatus* n. spm. Proximal view showing exposed nexine.
Figs. 44-45.—*M. fasciolatus* n. spm. Distal view showing furrow.
Fig. 46.—*Marsupipollenites* spm.

PERMIAN SPOROMORPHS



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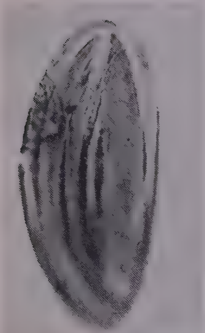
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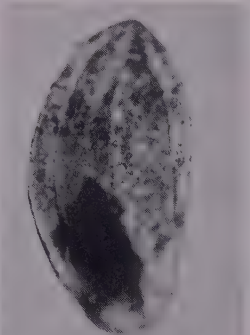
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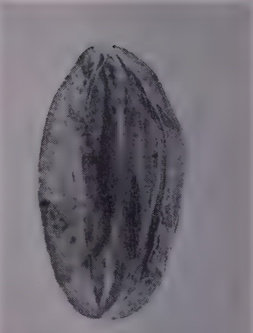
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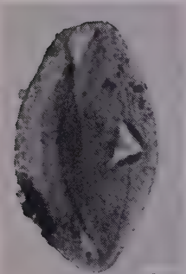
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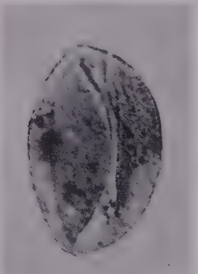
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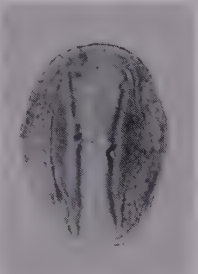
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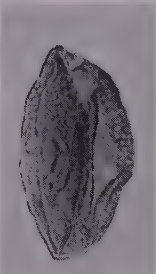
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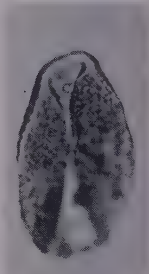
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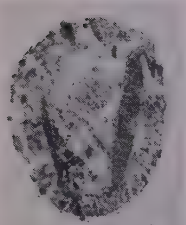
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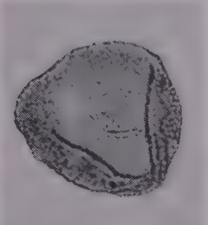
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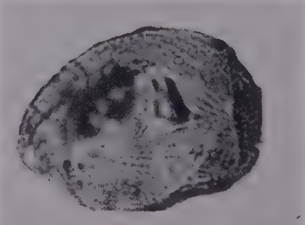
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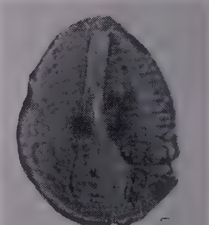
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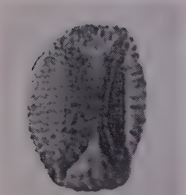
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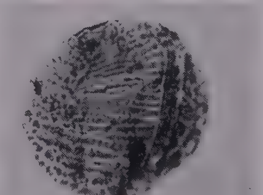
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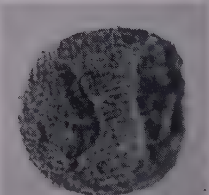
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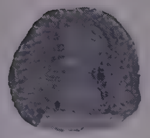
PERMIAN SPOROMORPHS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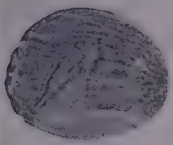
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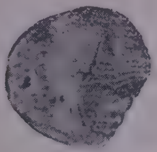
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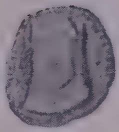
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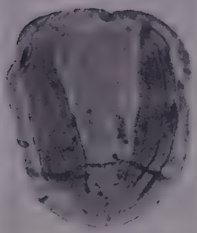
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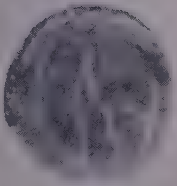
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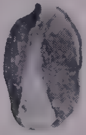
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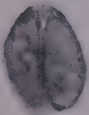
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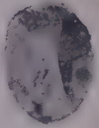
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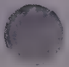
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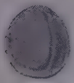
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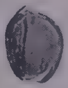
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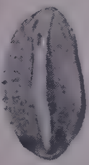
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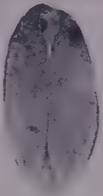
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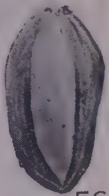
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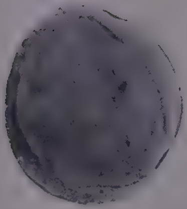
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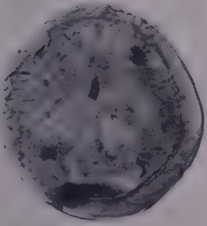
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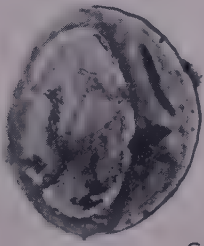
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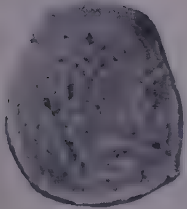
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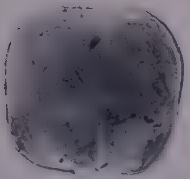
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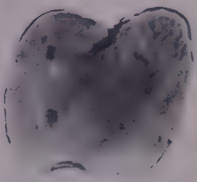
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Fig. 47.—*Marsupipollenites* spm. Distal view showing furrow.
Fig. 48.—*Marsupipollenites* spm.
Figs. 49-52.—*Entylissa vetus* n. spm. Distal view.
Fig. 53.—*Entylissa cymbatus* n. spm. Distal view, furrow margins overlapping at pole.
Figs. 54-56.—*E. cymbatus* n. spm.
Figs. 57-59.—*Pilasporites plurigenus* n. spm.
Figs. 60-61.—*Pilasporites calculus* n. spm. Intact grains.
Figs. 62-63.—*P. calculus* n. spm. Grains showing oval rupture in exine.
Fig. 64.—*P. calculus* n. spm. Exine granulate.
Fig. 65.—*P. calculus* n. spm. Exine rugose showing differential thickening.
Figs. 66-67.—*Incertae sedis.* Sporomorph "A".

SPECIES DISTRIBUTION OVER PART OF THE COONALPYN DOWNS, SOUTH AUSTRALIA

By W. H. Litchfield*

[*Manuscript received June 17, 1955*]

Summary

An account is given of edapho-climatic ranges and species area of elements of the mainly sclerophyllous vegetation of a representative portion of the Coonalpyn Downs. *Eucalyptus*, *Melaleuca*, *Acacia*, *Hakea*, *Leptospermum*, *Casuarina*, and *Callitris* are the principal genera discussed.

Water relations as governed by soil profile characteristics, landscape position, and the depth and salinity of water-tables are considered to be the main factors influencing plant distribution. The rainfall gradient across the area is gentle and rainfall as an independent factor only appears to influence water relations sufficiently to affect species distribution in a few cases. The fertility of soils on sandplain and sand dunes is invariably of a low order and a species composition typical of higher fertility soils is usually only found on inliers of such soils. Subsidiary edaphic responses include gross changes in soil reaction and soil salinity.

A few indicator species in a given plant community can be associated with some particular soil characteristic and such correlations are distinct from community responses. For example, *Hakea vittata* in heath is generally associated with sandplain soils with a lime pan or a calcic subsoil within 2 ft of the surface.

An examination of the area of numerous species shows that there is considerable variation across the territory in the composition of communities with repetitive dominants.

Evidence is presented that suggests that species migrations may have spread from refuges or at least continuously vegetated areas within the territory as well as from outside it. The poor correlation between the area or limits of centres of frequency of some species and their observed edapho-climatic ranges suggests that migration is still occurring and that the climax community has not been produced in all cases.

I. Introduction

The present paper is concerned primarily with the geography of single species and some aspects of their autecology in the remaining natural vegetation of 950 sq. miles of the Coonalpyn Downs of South Australia. A locality plan is shown in Figure 1.

The greater part of the synecology of the vegetation and some aspects of autecology of species in the four hundreds in County Buckingham (namely, Stirling, Pendleton, Cannawigara, and Senior) are recorded by Coaldrake (1951) and Specht (1951). The geography and morphology of the soils and the landscape pattern are shown more comprehensively by Blackburn *et al.* (1953). The soil and land use report of Jackson and Litchfield (1954) is the only† one dealing with the two hundreds in County Cardwell (Coombe and Richards).

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* Division of Soils, C.S.I.R.O., Adelaide.

† An unpublished soils and vegetation map of a large portion of the western side of the Coonalpyn Downs prepared by C. Melville, of the South Australian Department of Lands, takes in a small segment of the Hundred of Richards.

The data given here are taken mainly from the records of the above soil surveys together with certain recordings made by Coaldrake and given by personal communication. In addition to the above territory which is considered systematically, reference can sometimes be made to expansions of species area into adjacent parts of the Downs. The records were collected over a period extending from 1950 to 1953. As large-scale clearing operations were rapidly accelerated during this period and are expected to continue, these data should enlarge the records of the flora before it is largely destroyed.

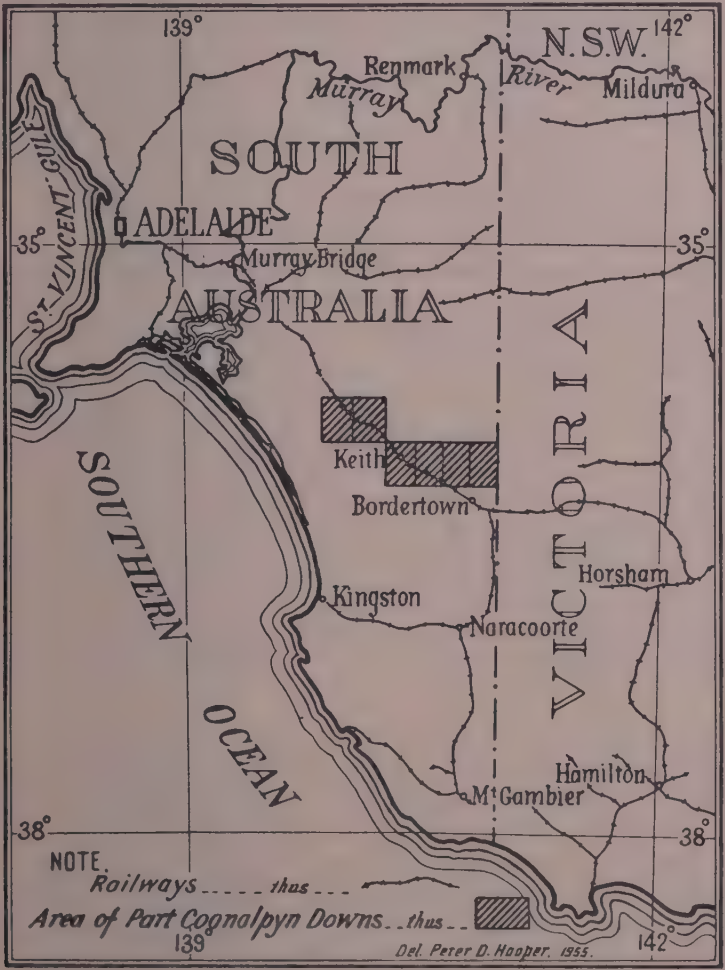

Fig. 1.—Locality plan showing area of Coonalpyn Downs, S.A., covered by species distribution charts.

II. ENVIRONMENT

(*a*) *Landscape and Associated Physical Features*

The area is largely sandplain together with very extensive systems of stabilized sand dunes, fixed largely by heath vegetation and ranging in size from low isolated rises to bunched ridges over 100 ft high. A number of "ranges" of travertinized consolidated dunes representing stranded Pleistocene shore-lines cut across the central hundreds in a direction roughly parallel to the present coastline. To the west of these ranges, substrata under sandplain are largely travertine limestone and sediments of variable texture which include only comparatively small areas of heavy clay. To the east, however, travertine is very rare and the proportion of deep heavy clay sediments much greater.

Other features include:

(i) inter-range travertine plain, with shallow loamy and calcareous soils;
(ii) plains and swales with clay soils with gilgai features;
(iii) a zone on the coastal side with salt-marshes and small salt lakes accompanied by adjoining plain areas with shallow saline water-tables;
(iv) shallow sand-choked valleys representing extensions of the gently dissected rolling landscapes of the Tatiara and Wimmera districts into the eastern hundreds;
(v) low hill systems near the Victorian border similar to others in western Victoria that are thought to be remnants of lateritic residuals;
(vi) a few granitic monadnocks of which Mt. Monster, south of Keith, is the most prominent; and
(vii) small seasonal swamps varying from flats with gilgai clay soils to depressions partially filled with sand.

(*b*) *Soils*

The morphology and geography of the soils are adequately described in earlier publications. Halomorphism, calcimorphism, and hydromorphism in varying combinations dominate soil morphology, excepting amorphic types.* Solodic and solonetzic features in the soils are of widespread occurrence.

Nutritional levels are very low by agronomic standards in the sandplain soils (see Riceman 1948) but are appreciably higher in the shallow calcareous soils and certain minor swamp soils. The greater proportion have alkaline subsoils and contain lime either in the subsoil or substratum.

The principal soil groupings can be outlined conveniently as shown in Table 1. It is expedient to name these groupings to facilitate further reference. In most cases, the name follows from that of a soil association in which the group is dominant. Table 1 indicates the prominent characteristics which the soils of each group have in common.

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* The terminology used here is based on that employed by Stephens (1953*a*, 1953*b*). The general status of unclassified groupings can usually be covered by adaptations from his terminology or classification.

TABLE 1

CHARACTERISTICS, LAND FORM, AND PARENT MATERIALS OF THE PRINCIPAL SOIL GROUPINGS

Soil Group	Soil Characteristics	Land Form and Parent Material
Keith group	Shallow loamy calcareous soils of less than 1 ft depth. Degraded variants are differentiated into thin, light, and heavier-textured horizons. They range from grey calcareous soils to others in the direction of terra rossa	Plain; on massive travertine
Culburra group	Similar soils to the Keith group (particularly the browner types) except for their unconsolidated substrata. The nature of the calcareous horizon is close to that found in some mallee soils	Plain; on marl or travertine rubble
Laffer group	Degraded calcimorphic soils with a grey sandy A_1 horizon* and a bleached A_2 horizon generally abruptly changing at 4-12 in. depth to a yellow or brown friable calcic heavier-textured B horizon. In poorly developed profiles, which become prominent on the coastal side, the B horizon may be very thin, and the travertine may occur as discontinuous boulders	Sandplain; on travertine
Coombe group	Similar soils to the Laffer group except for their unconsolidated substrata	Sandplain; on marl or travertine rubble
Brimbago group	Terra rossa and degraded terra rossa; such soils generally occur in small pockets only	"Range" slopes and hillocks; chiefly lower slopes; on travertine
Kumorna group	Degraded calcimorphic soils with a deeper sandy A horizon than that of the Laffer soils. The B horizon is represented by erratically distributed coarse-textured but clayey deposits and lime in various forms	Inter-range sandplain and swales; on coarse-textured sediments
Richards group	Soils similar to the Kumorna group except that they show gley effects and solonization of the B horizon due to the influence of underlying saline water-tables. Such soils can be given the status of degraded hydro-halomorphic types	Inter-range sandplain and swales; on coarse-textured sediments
Shaugh group	Solodic soils with deep (2-4 ft) sandy A horizons over stiff mottled B horizons of variable texture (generally sandy clay loam to clay). The occurrence of lime in the deeper subsoil is discontinuous	Sandplain and swales mainly east of the "ranges"; largely on arenaceous clay beds

* The horizon notation is the simple one used, for example, by Leeper (1948).

TABLE 1 (*Continued*)

Soil Group	Soil Characteristics	Land Form and Parent Material
Colebatch group	Soils similar to the Shaugh group except that the subsoil is generally coarser textured and more friable. An erratic distribution of travertine "floaters" is sometimes found	Undulating inter-range areas and swales; on coarse-textured sediments
Buckingham group	Solodized solonetz with sandy A horizons (generally of 6-12 in. depth) and tough columnar yellowish clays with some mottling. Variants range from the more calcimorphic types with marly B_2 horizons to soils free from lime. Large amounts of flinty lime associated with salts in the deep subsoil are not accompanied by much amelioration of the clay	Sandplain and swales; on clay beds
Red Bluff group	Sandy solodic soils, often lime free, characterized by tough reddish mottled clay and subsoils and heavy ferruginous nodule segregation in the A_2 horizon	Slopes of the low hill systems east of the "ranges"; on clay beds
Berangwee group	Lateritic podzolic soils (?) with an ironstone horizon between the sandy A horizon and a bright mottled clayey B horizon	Margins of some of the shallow valleys east of the "ranges"; largely on sandy clays
Senior group	Grey soils of heavy texture of the gilgai areas in mallee scrub. Large depressions, some with "runaway" holes, and marginal puffs with lime rubble are characteristic of these soils	Gilgai plains and swales on heavy clays east of the "ranges"; on clay beds
Wirrega group	Gilgaied grey soils of heavy texture under sedge-savannah in swampy areas characterized by their shelf microrelief with small discrete puffs of self-mulching soils	Semi-swamp areas on the east side of certain range formations (of very restricted occurrence in the territory but similar soils are more common over some of the poorly drained flats in the Tatiara and Wimmera Districts); on clay beds
Willyama group	Highly calcareous brownish gilgai soils with very large amounts of lime rubble on and in the puffs and at shallow or moderate depth in the depressions. Their status lies perhaps between mallee soil and brown soils of heavy texture	Low parts of inter-range corridors (of restricted occurrence); on (?) calcareous clays

TABLE 1 (*Continued*)

Soil Group	Soil Characteristics	Land Form and Parent Material
Cannawigara group	Solonetz soils fringing many of the gilgai areas with thin brown coarse-textured A horizons of 1·6 in. depth and tough, columnar brownish or yellowish mottled clays	Fringes of plains and swales with gilgais east of the "ranges"; on clay beds
Monkoora group	Ground-water (gleyed) solonetz with sandy alkaline A_1 and A_2 horizons, a strongly gleyed columnar B horizon, and variable calcareous substrata with a saline water-table	Inter-range saline sandplain; on sediments of variable texture
Lake Ellen group	Shallow solonchaks of the saline swamps and salt lakes; they are usually dark salt-flocculated soils with highly calcareous or gypseous deposits. A variant, superficially resembling a rendzina, has an almost black nutty-structured clay horizon a few inches deep	Salt lakes and marsh; on sediments of variable texture
Skeletal soils A (unnamed group)	Very shallow soils amongst travertine on the "ranges" which have been exposed by erosion	Stony travertine slopes of the "ranges"
Skeletal soils B (unnamed group)	Loamy soils amongst the granite outcrops. Small pockets with clay subsoil and lime horizons are found	Granite hills and hillocks
Aeolian sands (unnamed group)	The grey A_1 horizons pass into a thin white subsurface horizon and thence into deep almost undifferentiated pale yellow sand	Sand dunes

(c) *Climate*

The Mediterranean climate of the area is marked by gentle rainfall gradients across the territory decreasing from the coast towards the inland. Most parts lie within the 18 and 20 in. isohyets and the extremes are probably of the order of 17½-21 in. (Blackburn *et al.* 1953). Statistics for rainfall, temperature, and wind velocity and direction are presented in the earlier publications.

III. ECOLOGICAL AMPLITUDES AND SPECIES AREA

Species and community variation are of a high order both numerically and geographically within the territory. As the climatic gradients and changes in soil fertility are apparently slight over large tracts, it is considered that the internal water relations of the soils or their substrata are often the prime factor governing the distribution of many of the larger plants. This generalization thus supports the field conclusions of Coaldrake (1951) and the thesis is expanded herein from field observations. The main controls influencing water relations are believed to be not

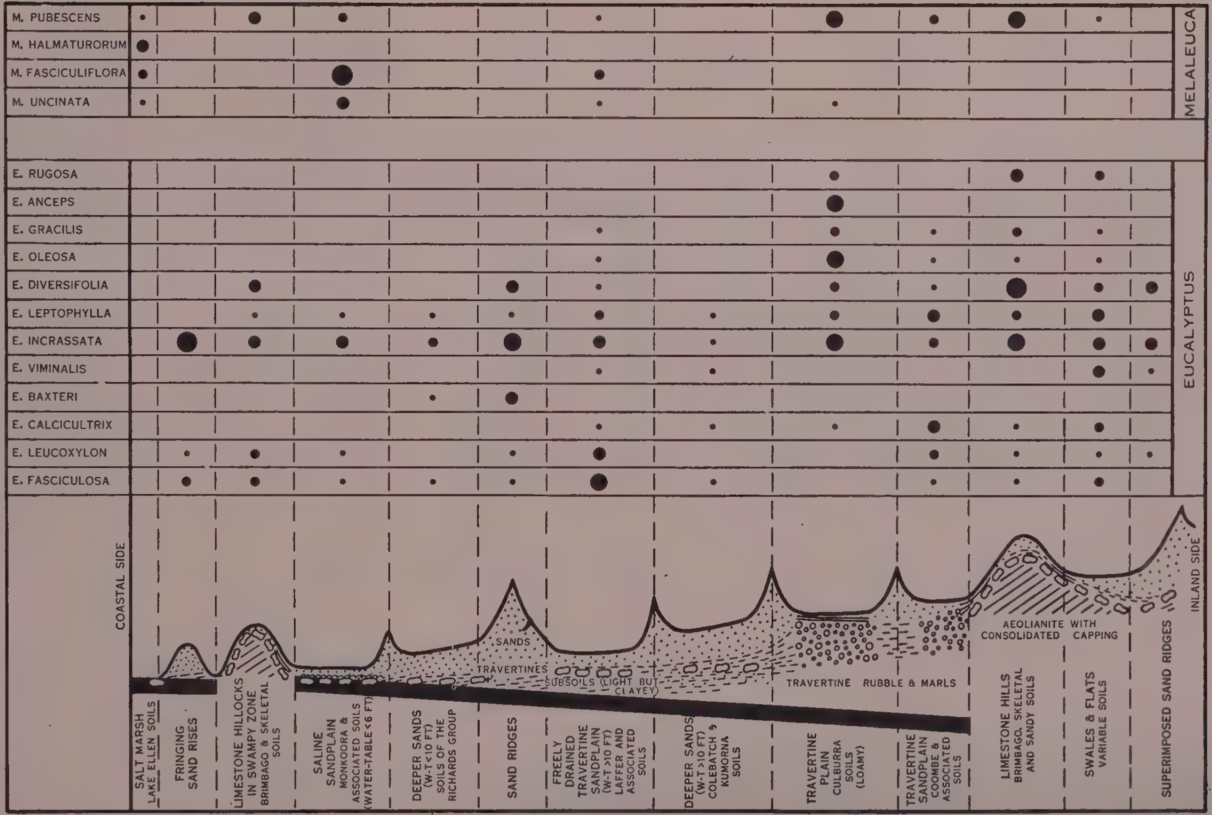
MELALEUCA
M. PUBESCENS
M. HALMATURORUM
M. FASCICULIFLORA
M. UNCINATA
EUCALYPTUS
E. RUGOSA
E. ANCEPS
E. GRACILIS
E. OLEOSA
E. DIVERSIFOLIA
E. LEPTOPHYLLA
E. INCRASSATA
E. VIMINALIS
E. BAXTERI
E. CALCICULTRIX
E. LEUCOXYLON
E. FASCICULOSA
COASTAL SIDE
INLAND SIDE
SANDS
TRAVERTINES
SUBSOILS (LIGHT BUT CLAYEY)
TRAVERTINE RUBBLE & MARLS
AEOLIANITE WITH CONSOLIDATED CAPPING
SALT MARSH LAKE ELLEN SOILS
FRINGING SAND RISES
LIMESTONE HILLOCKS IN SWAMPY ZONE BRIMBAGO & SKELETAL SOILS
SALINE SANDPLAIN MONKOORA & ASSOCIATED SOILS (WATER-TABLE < 6 FT)
DEEPER SANDS (W-T < 10 FT) SOILS OF THE RICHARDS GROUP
SAND RIDGES
FREELY DRAINED TRAVERTINE SANDPLAIN (W-T >10 FT) LAFFER AND ASSOCIATED SOILS
DEEPER SANDS (W-T >10 FT) COLEBATCH & KUMORNA SOILS
TRAVERTINE PLAIN CULBURRA SOILS (LOAMY)
TRAVERTINE SANDPLAIN COOMBE & ASSOCIATED SOILS
LIMESTONE HILLS BRIMBAGO, SKELETAL AND SANDY SOILS
SWALES & FLATS VARIABLE SOILS
SUPERIMPOSED SAND RIDGES

Fig. 2.—A diagrammatic representation of the relative frequencies of the species *Eucalyptus* and *Melaleuca* correlated with the major habitats in the Hundreds of Richards and Coombe, S.A. The larger the figure, the higher the frequency and/or percentage occupation of a given habitat (observational estimates only).

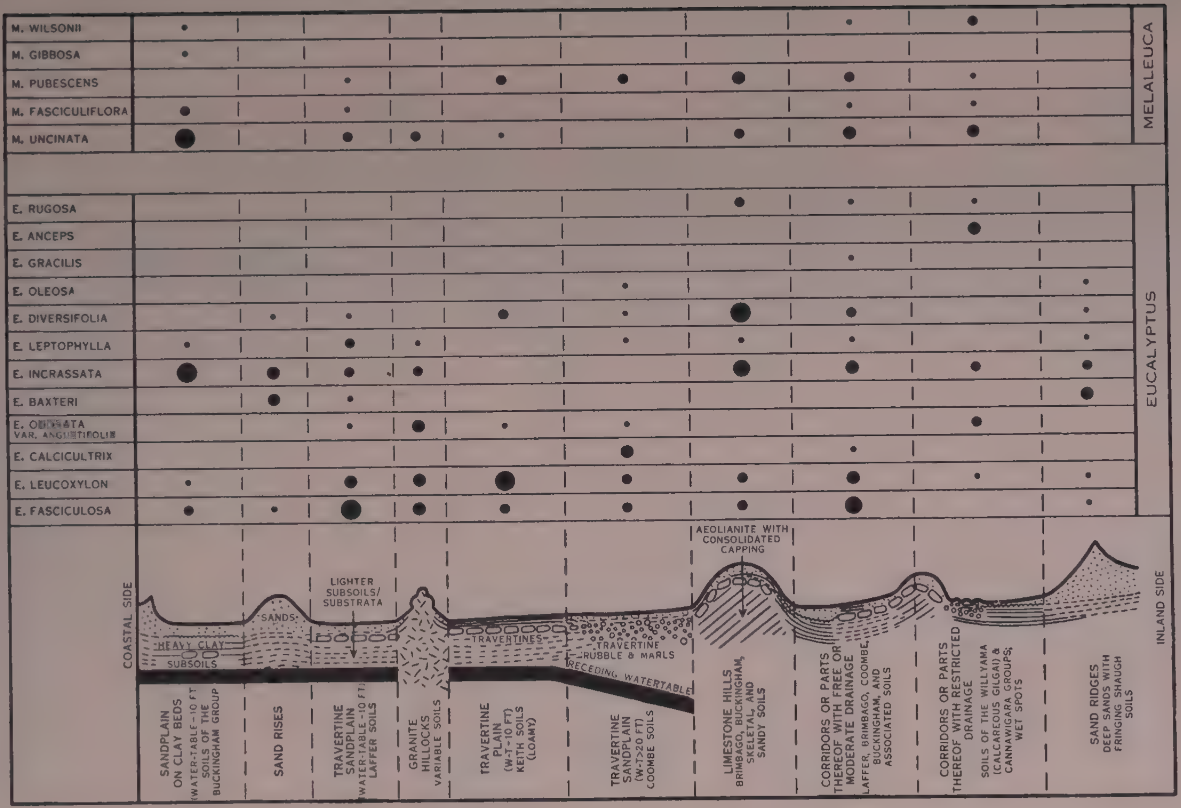

Fig. 3.—A diagrammatic representation of the relative frequencies of the species *Eucalyptus* and *Melaleuca* correlated with the major habitats in the Hundreds of Stirling and Pendleton, S.A. The larger the figure, the higher the frequency and/or percentage occupation of a given habitat (observational estimates only).

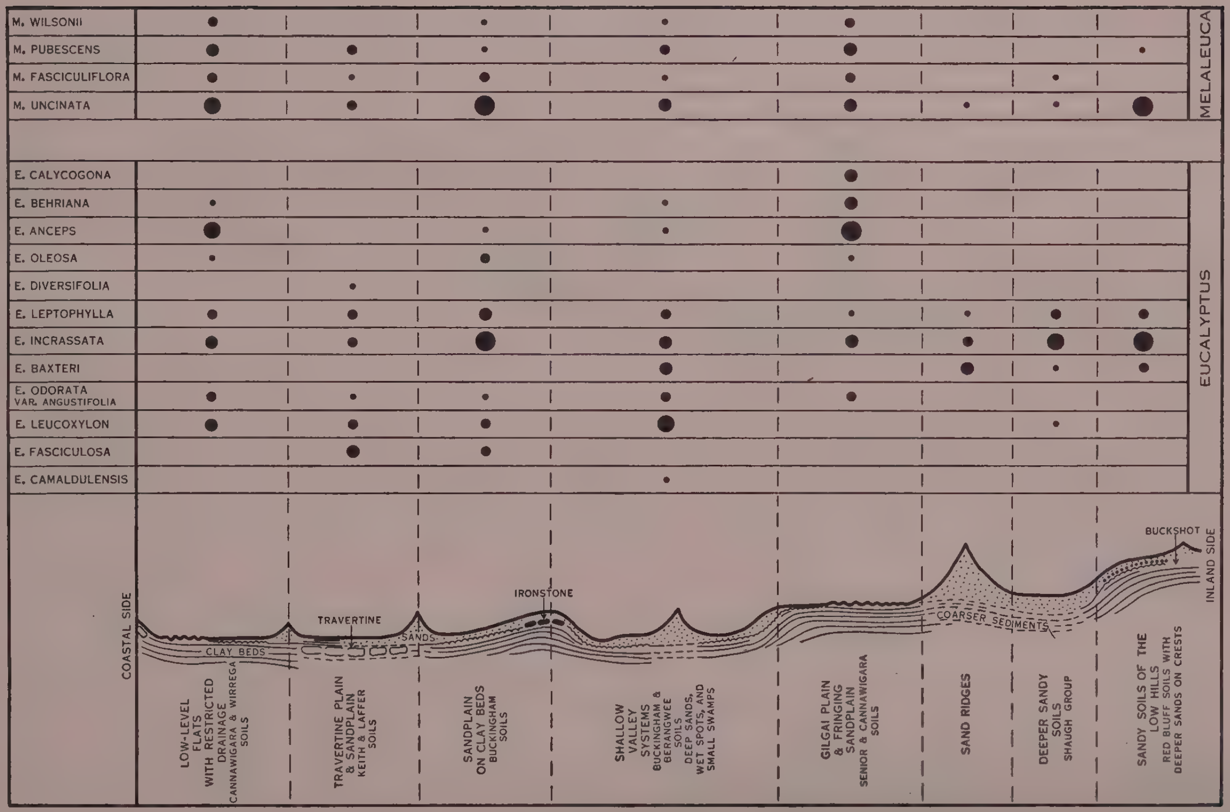

Fig. 4.—A diagrammatic representation of the relative frequencies of the species *Eucalyptus* and *Melaleuca* correlated with the major habitats in the Hundreds of Cannawigara and Senior, S.A. The larger the figure, the higher the frequency and/or percentage occupation of a given habitat (observational estimates only).

only the physical characteristics of the soils but also their landscape position and levels of widespread or locally perched water-tables. Additional edaphic controls probably include salinity levels, soil reaction, and/or the lime status, and in a few cases, fertility levels. The regional rainfall amplitude as such is also believed to influence species distribution in a few cases, judging from the extraneous position of their stations in relation to species area and rainfall gradients. The influence of the last factor is, however, difficult to isolate from edaphic and hydrological influences.

Diagrammatic representations of the frequency of the species of *Eucalyptus* and *Melaleuca* in the major habitats of the six hundreds are shown in Figures 2-4. The pattern of distribution of the species of recorded vegetation has been plotted on a series of maps in Charts 1-9. Appendix I lists native plants recorded.

(*a*) Eucalyptus (*Charts* 1-3)

Eucalyptus provides dominant or co-dominant species for the majority of communities in savannah woodland, dry sclerophyll woodland, mallee scrub (including "mallee-broombush"), and mallee-heath. Heaths, scrubs dominated by *Melaleuca*, and salt-marsh represent the remainder of the formations or subformations. *Casuarina*, excepting *C. pusilla* as a co-dominant species in heath, and *Callitris* rarely reach frequencies that provide dominants for communities.

It is evident that the tolerances of a number of species are severely taxed within their species area. The prevalence of mallee forms in a climatic zone where woodland might be expected to occur generally is indicative of edaphic stress (Wood 1950). Although eucalypt trees reach a maximum height of about 40 ft in savannah woodland and other especially favoured stations, depauperation of both tree and mallee growth is very widespread in sclerophyllous communities. *E. leucoxylon*, *E. viminalis*, and *E. baxteri* can all exhibit a mallee habit and *E. fasciculosa* may likewise become very stunted. All other species, excepting *E. camaldulensis*, but including *E. calcicultrix* and *E. odorata* var. *angustifolia*, are found only as mallees.

Extreme depauperation is often reached by species such as *E. incrassata*, *E. diversifolia*, and *E. leptophylla* in a broad zone extending diagonally across the Downs from the south-western side of County Cardwell to the northern hundreds of County Buckingham and parts of the adjacent counties of the "Big Desert" in Victoria. These mallees are here often reduced to mere shrubs 2-4 ft high. The limits of the belt cannot be wholly accounted for either from the spread of rainfall isohyets or from soil characteristics. Other sandy parts of the region with similar rainfall gradients, such as some of the eastern hundreds in County Buckingham and the "Bangham scrub" area, have much more marked contrasts in vegetation and include many areas of well-grown mallee-heath or sclerophyll woodland. It is considered probable that the stunting can arise from both physiological drought* and climatic drought. Near the coast, stunting may arise from osmotic stresses due to exploratory roots reaching the highly saline water-tables (frequently 1700-2900 parts of soluble salts per 100,000 parts of water at depths of less than 10 ft from the surface). Jessup (1946) has referred to a case where certain heath species, but no eucalypts, persist in saline hollows between coastal sandhills. It is likely that this control, with a moderating influence, continues inland through the zone with relatively shallow saline ground-waters. Thus heath usually persists in these areas but the deeper rooting eucalypts are retarded or eliminated. One apparent response to release from high salinity in this zone is the presence of very sharply defined fringing communities of some of the larger eucalypts such as *E. baxteri* and *E. fasciculosa* around the margins of seasonal lakes of fresh water with a sedge-meadow floor. These occur in the south-western parts of the Downs in hundreds such as Messent and the south-west side of McNamara. The ponding areas are created by floodwaters coming up the inter-range corridors from the south in wet seasons. Well-grown mallee and gums are also found in places around some of the salt lakes and saline sandplains, and it would be interesting to know if there are any variations in the quality of the ground-water in such places; there are at present no records. Stunted mallee and very occasionally gums enter some of the *Melaleuca fasciculiflora* communities on saline sandplain with Monkoora soils, and this environment thus appears to border limits of tolerance of *Eucalyptus* towards waterlogging and high salinity. On high dunes and generally in inland areas stunting probably arises directly from moisture stresses.

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* Dr. N. C. W. Beadle (personal communication) has pointed out that the behaviour of these species may be influenced by their ability or otherwise to act as chloride accumulators. There are at present no pertinent data relative to these species.

The species are named according to Burbidge (1947) with the exception of *E. incrassata*.* Difficulties were also experienced on occasion with field identification between the following species pairs: (1) *E. incrassata* and *E. anceps*, (2) *E. anceps* and *E. rugosa*, (3) *E. leucoxylon* and *E. fasciculosa*, (4) *E. leucoxylon* and *E. calcicultrix*, and (5) *E. calcicultrix* and *E. odorata* var. *angustifolia*. *E. viminalis* occurs in a rough-barked form.

(i) E. fasciculosa (*Chart* 1).—The species has a wide distribution over the central and western portions of the territory. The frequency of stations, however, rapidly diminishes to the east of the easternmost "ranges" and travertine sandplains in the Hundreds of Pendleton and Cannawigara. The margin of area nowhere extends more than a few miles further east. This distribution is thus a transect across the species area in coastal South Australia which extends from County Robe in the lower south-east (Crocker 1944) to Kangaroo Island (Northcote and Tucker 1948) and the Mt. Lofty Ranges (Specht and Perry 1948). There are apparently no very wide disjunctions,† the Murray Lakes area probably being the most significant.

The species generally forms some type of sclerophyll woodland with extensions into ecotones with savannah woodland, where sedges are often prominent in the ground flora. The most numerous centres of frequency occur on sandplain soils over travertine, especially those of the Laffer group, with free to moderate drainage. The majority of well-established communities occur where free soil drainage is coupled with indications of relatively favourable water-supply. It is likely that exploratory roots reach the relatively shallow water-tables under travertine plain. Depth to water in wells in woodland in open plain is generally less than about 25 ft. The topographic position of communities fringing the lower flanks and gullies of ranges and adjacent strips of plain or corridors, of those near high dunes, and of those on well-drained low rises fringing saline swamps, freshwater swamps, and other wet spots are all suggestive of locally increased underground moisture supply.

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* *E. incrassata* and *E. angulosa* are treated together as one species. This approach is thus consistent with that of J. E. Coaldrake (1951).

† This term and a number of others which are used herein and are related to species area are defined by Cain (1944).

The species appears on occasion to be very sensitive to edaphic conditions. It generally either avoids or does not compete against the vegetation on the shallow calcareous soils of the Keith and Culburra groups and the deep aeolian sands. It has only a low ability to occupy the higher sand ridges, although occasionally stations in County Cardwell are found almost at the top of the slip slope. Tolerance of periodically waterlogged, saline sandplain soils in the Monkoora group is low and invasion of *Melaleuca fasciculiflora* stands rare. The species has only a limited ability to occupy soils of the Buckingham group where elements of mallee-broombush vegetation are generally well established. Where the soils of the Laffer and Buckingham groups lie in juxtaposition in the Hundreds of Stirling and Pendleton, woodlands are of very limited extent on varieties of the Buckingham soils with the toughest and most impermeable clays. Such soils are much more widespread in the eastern hundreds. The prevalence of such soils together with sand dunes and gilgai soils, and the existing occupation of wet hollows by *E. leucoxylon* are probably together acting as a substantial barrier against outward migration in this direction.

(ii) E. leucoxylon (*Chart* 1).—Although *E. leucoxylon* has a wide species area in the territory, edaphic stresses result in a wide spacing of stations in parts. Considering its species area in South Australia and western Victoria as a whole, it has fairly wide climatic and edaphic tolerances therein. Its most widespread development is in savannah woodland within the rainfall bracket of 18-30 in. Extraneous occurrences are, however, reported on heavy soils as far inland as the southern parts of the Western Division of New South Wales (Anderson 1947; Carter, n.d.). Carter shows also the species area extending inland through western and north-western Victoria. This territory and its environs exemplifies the ability of the species to extend beyond savannah woodlands into the adjacent sandy tracts of low fertility soils supporting sclerophyllous communities. The savannah centres are marked out by the various medium and heavy textured soils in the Tatiara (Specht 1951) and Wimmera districts, and similar edaphic refuges in the territory such as the Keith soils. There are many indications that stations in the sandy tracts usually have locally improved water relations. Apart from the Keith area, important centres of frequency include shallow valley floors and some hillsides in the Hundred of Cannawigara and the southern part of the Hundred of Senior with Buckingham soils, the travertine plains near Tintinara and the west side of Cannawigara Siding with Keith or Laffer soils, sandy soils on the mid and lower slopes of Mt. Monster, Wirrega swamp soils south of Wirrega, and a few centres on Brimbago terra rossa in the "range" formations. Fertility levels are probably superior to many other types in the three last-named groupings. Ability to colonize sand dunes is of a low order, although a dwarfed mallee variety is occasionally found high up on the slip slope in County Cardwell. Depauperation into a mallee habit is common in areas where edaphic stresses could well be near the limits of tolerance, for example, in swales with soils with excessive internal drainage in and near the ranges of north-eastern Coombe and on the deep sandy solods of the Shaugh group bordering woodlands in the eastern hundreds. Extraneous stations are known to extend north-eastwards as far inland as low spots in the hills with Red Bluff soils near Red Bluff Hill (a lateritic residual lying 36 miles due north of Serviceton), and further north to 6 miles south of Murrayville (Zimmer 1946) where the rainfall drops to 12·6 in.

A conspicuous feature of the distribution is the presence of *E. leucoxylon* and *E. leucoxylon-E. fasciculosa* woodlands around Keith and Tintinara which contrast with the remnants of mallee scrub extending from near Tintinara to Culburra and likewise north-west of Keith in the direction of Sugar Loaf Hill. Rainfall appears to be virtually uniform in these areas and the soils are similar in many respects. There are, however, two differences in habitat between the two formations, namely, (1) differences in water-table levels which lie at about 10 ft near Keith and even less near Tintinara as compared to appreciably greater depths under mallee (at places 25-40 ft) and (2) differences in the characteristics of the calcareous substrata under the soils which are usually massive travertine in the Keith and Laffer group soils and porous rubbles and marls in the Culburra and Coombe soils.

Although *E. fasciculosa* and *E. leucoxylon* coexist in many woodland communities, both are often sensitive to small differences in habitat and tend to segregate into localized types. *E. leucoxylon* often occupies the wetter and lower spots and soils with shallower water-tables and higher salinity levels. A clear-cut expression of a zonal distribution of the two species is sometimes found fringing saline swamp or saline sandplain.

(iii) E. viminalis *syn.* E. huberiana *N.T. Burbidge.*—The species area in the northern and eastern parts of the Hundred of Coombe shows the ability of the species to colonize freely on excessively drained sandy soils at the lower limits of its rainfall range. This portion of its edapho-climatic range thus parallels that of *E. baxteri* to some extent, and it is peculiar that their respective areas barely overlap here. There is no published record of this distribution which reduces the recorded disjunctions between the Mt. Lofty Ranges and other areas in the mid and lower south-east and the extensive regional occurrences throughout the woodlands and sclerophyll forests of south-eastern Australia. The nearest recordings in the mid south-east are in sclerophyllous woodland communities near Naracoorte and Lucindale (Crocker 1944) and in a stunted form near Kingston on an undulating sandplain (Blackburn 1952).

The distribution consists mainly of small pockets of sclerophyll woodland amongst stunted mallee and heath in high sand ridges and range corridors. Individual communities often show a mixture of tree and mallee forms. Local centres of frequency are often centred in sandy swales with individuals with a mallee habit extending the distribution on to slip slopes. Odd well-grown trees enter the margin of woodlands of *E. fasciculosa* with some *E. leucoxylon* and *E. calcicultrix* on well-drained Laffer soils fringing the sand ridges near the range formations.

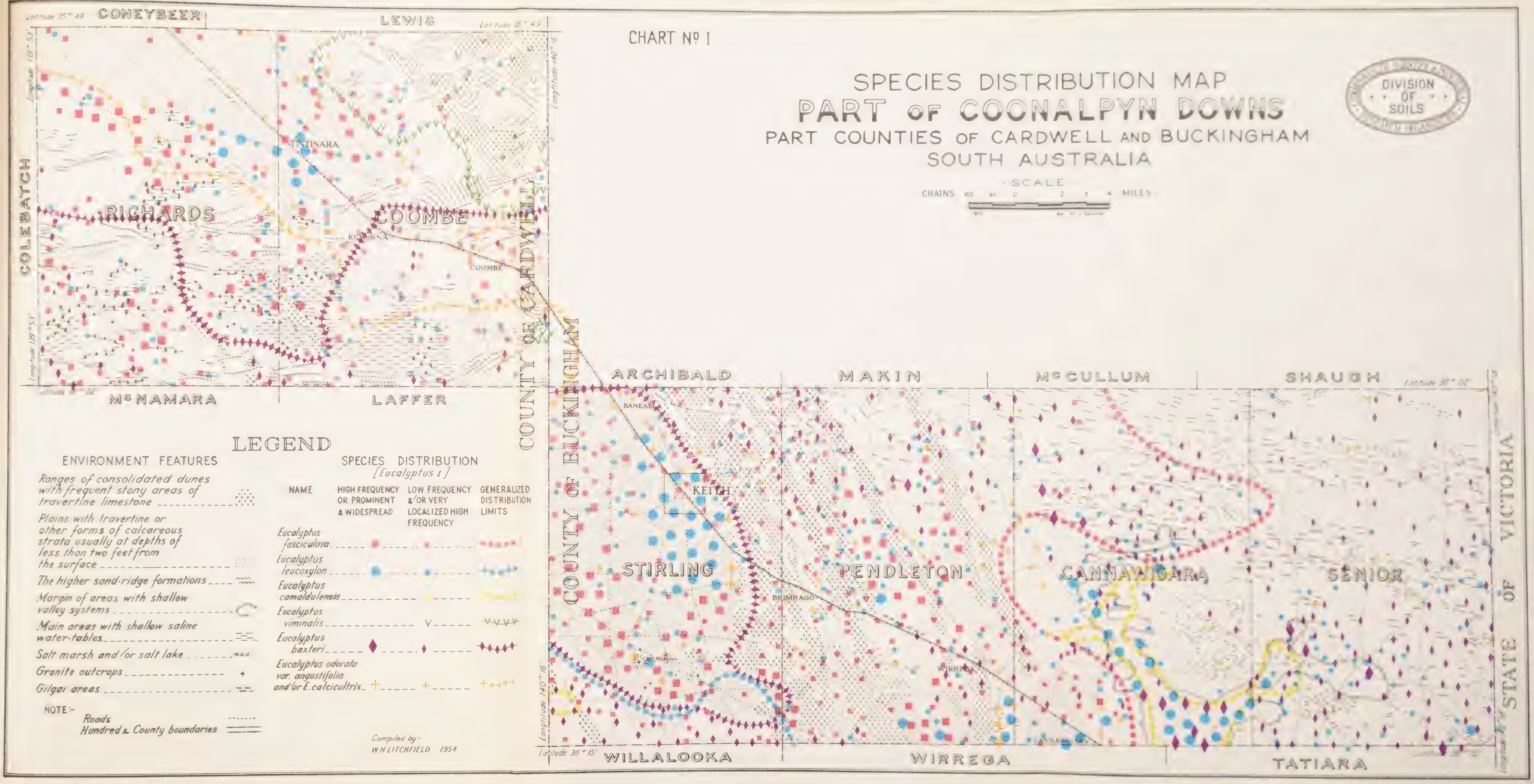


CHART Nº 1
SPECIES DISTRIBUTION MAP
PART OF COONALPYN DOWNS
PART COUNTIES OF CARDWELL AND BUCKINGHAM
SOUTH AUSTRALIA
SCALE
CHAINS 160 80 0 1 2 3 4 MILES
DIVISION OF SOILS
CONEYBEER
LEWIS
COLEBATCH
RICHARDS
COOMBE
TINTINARA
KULKONA
COUNTY OF CARDWELL
COUNTY OF BUCKINGHAM
McNAMARA
LAFFER
ARCHIBALD
MAKIN
McCULLUM
SHAUGH
BANEALLA
KEITH
STIRLING
PENDLETON
CANNAWIGARA
SENIOR
BRIMBAGO
WIRREGA
WILLALOOKA
TATIARA
STATE OF VICTORIA
Latitude 35° 49'
Latitude 36° 02'
Latitude 36° 15'
Longitude 139° 53'
Longitude 140° 16'
LEGEND
ENVIRONMENT FEATURES
Ranges of consolidated dunes with frequent stony areas of travertine limestone
Plains with travertine or other forms of calcareous strata usually at depths of less than two feet from the surface
The higher sand-ridge formations
Margin of areas with shallow valley systems
Main areas with shallow saline water-tables
Salt marsh and/or salt lake
Granite outcrops
Gilgai areas
NOTE:- Roads
Hundred & County boundaries
SPECIES DISTRIBUTION [Eucalyptus 1]
NAME
HIGH FREQUENCY OR PROMINENT & WIDESPREAD
LOW FREQUENCY &/OR VERY LOCALIZED HIGH FREQUENCY
GENERALIZED DISTRIBUTION LIMITS
Eucalyptus fasciculosa
Eucalyptus leucoxylon
Eucalyptus camaldulensis
Eucalyptus viminalis
Eucalyptus baxteri
Eucalyptus odorata var. angustifolia and/or E. calcicultrix
Compiled by:- W.H. LITCHFIELD 1954

Chart No. 1.—Species distribution—*Eucalyptus* 1.

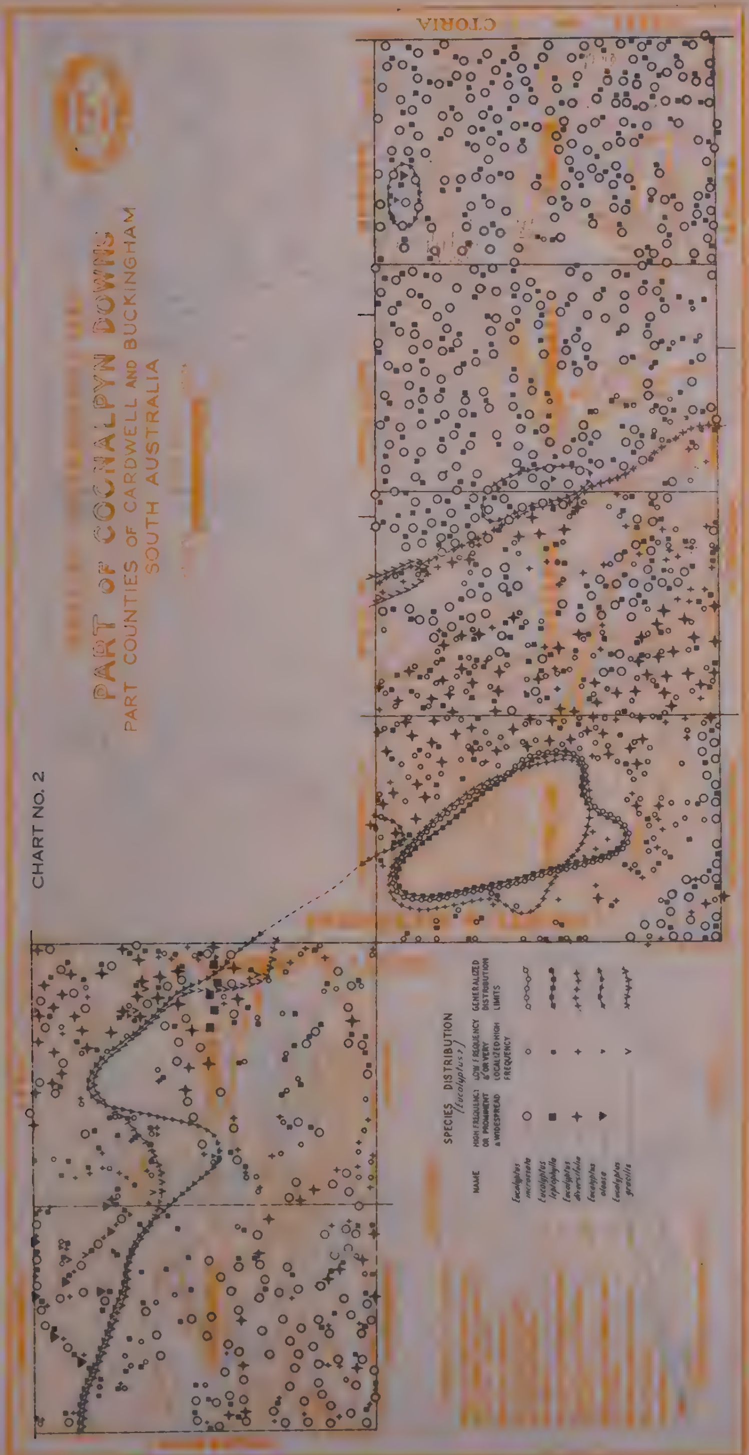


Chart No. 2.—Species distribution—*Eucalyptus*.

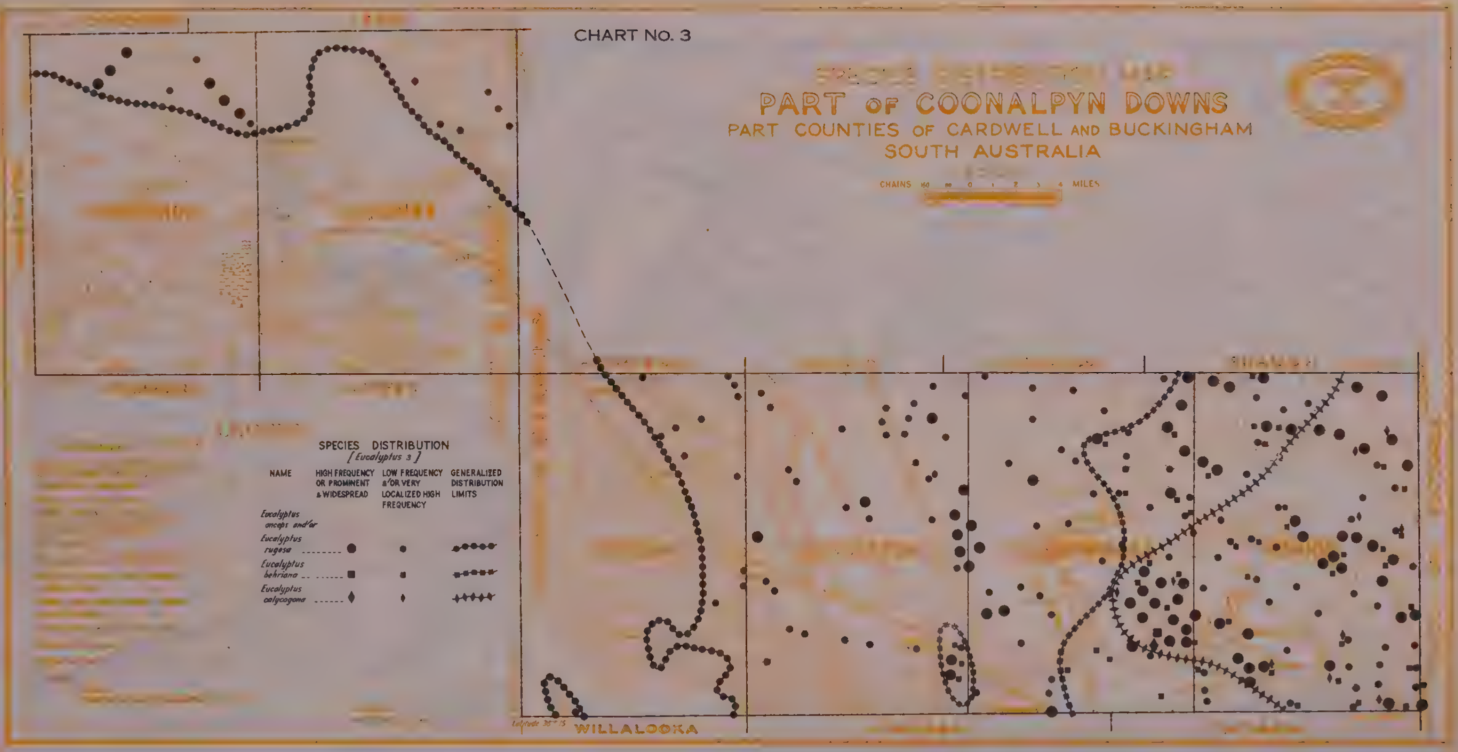


CHART No. 3
PART OF COONALPYN DOWNS
PART COUNTIES OF CARDWELL AND BUCKINGHAM
SOUTH AUSTRALIA
CHAINS 160 80 0 1 2 3 4 MILES
SPECIES DISTRIBUTION
[Eucalyptus 3]
NAME
HIGH FREQUENCY OR PROMINENT & WIDESPREAD
LOW FREQUENCY &/OR VERY LOCALIZED HIGH FREQUENCY
GENERALIZED DISTRIBUTION LIMITS
Eucalyptus anceps and/or
Eucalyptus rugosa
Eucalyptus behriana
Eucalyptus calycogona
WILLALOOKA

Chart No. 3.—Species distribution—*Eucalyptus* 3.

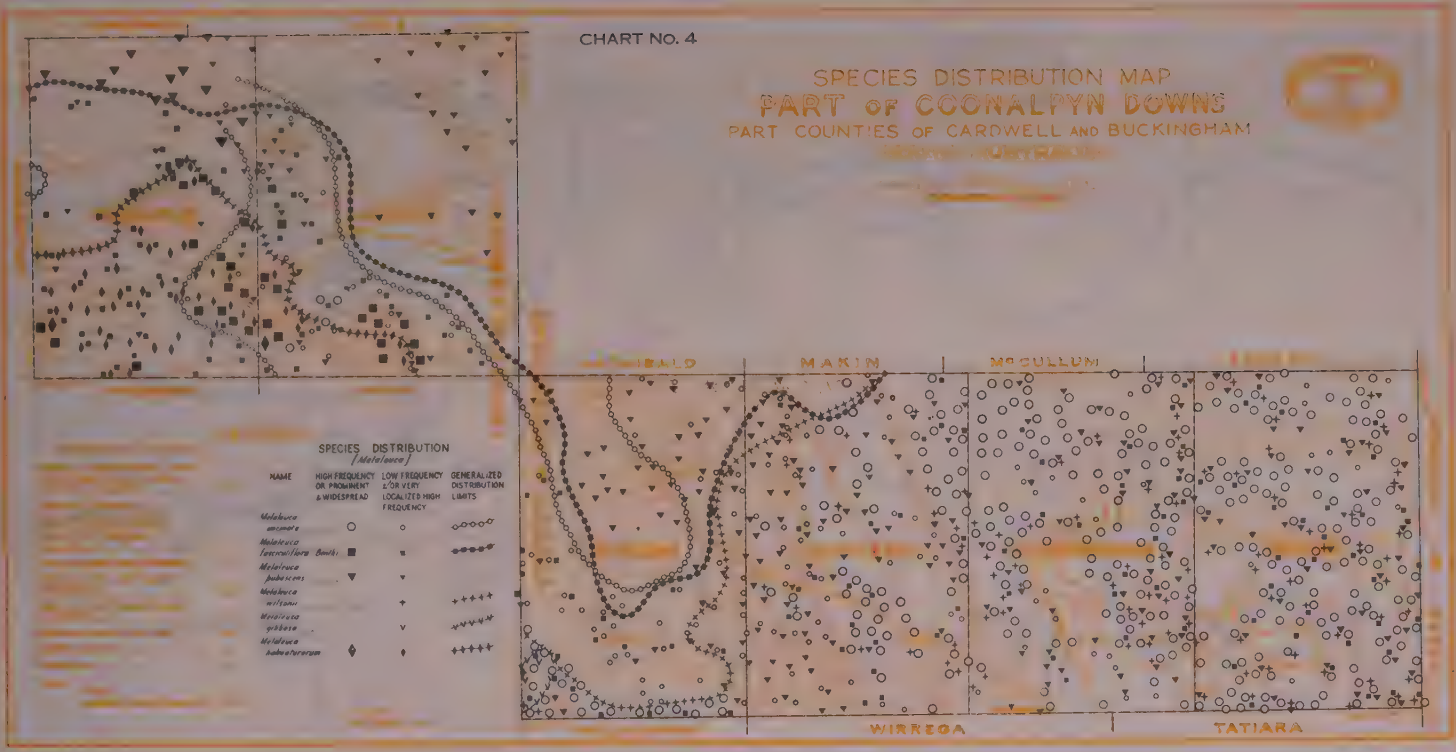


Chart No. 4.—Species distribution—*Melaleuca*

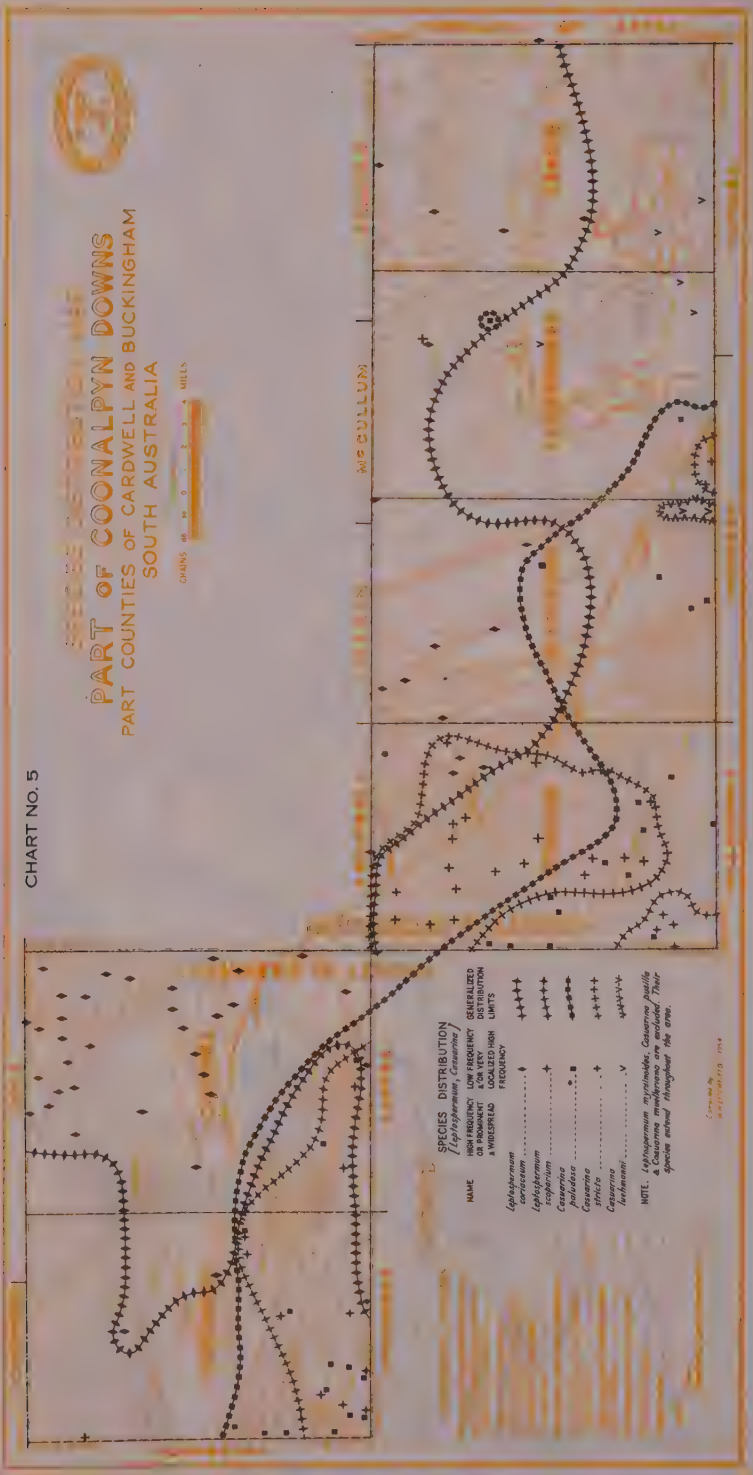


CHART NO. 5
PART OF COONALPYN DOWNS
PART COUNTIES OF CARDWELL AND BUCKINGHAM
SOUTH AUSTRALIA
CHAINS 60 80 0 2 4 MILES
McCULLUM
SPECIES DISTRIBUTION
[Leptospermum, Casuarina]
NAME
HIGH FREQUENCY OR PROMINENT & WIDESPREAD
LOW FREQUENCY &/OR VERY LOCALIZED HIGH FREQUENCY
GENERALIZED DISTRIBUTION LIMITS
Leptospermum coriaceum
Leptospermum scoparium
Casuarina paludosa
Casuarina stricta
Casuarina luehmanni
NOTE. Leptospermum myrsinoides, Casuarina pusilla & Casuarina muelleriana are excluded. Their species extend throughout the area.

Chart No. 5.—Species distribution—*Leptospermum, Casuarina.*

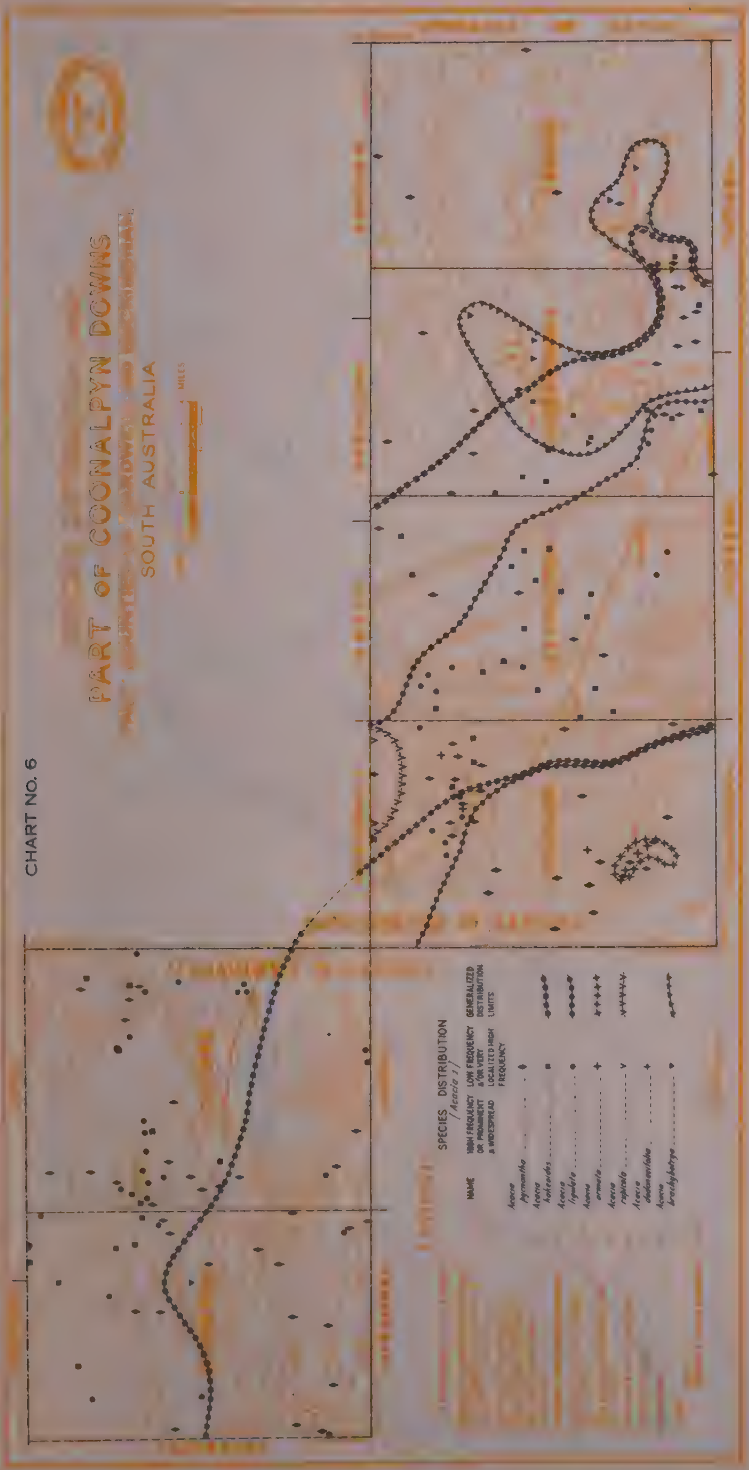
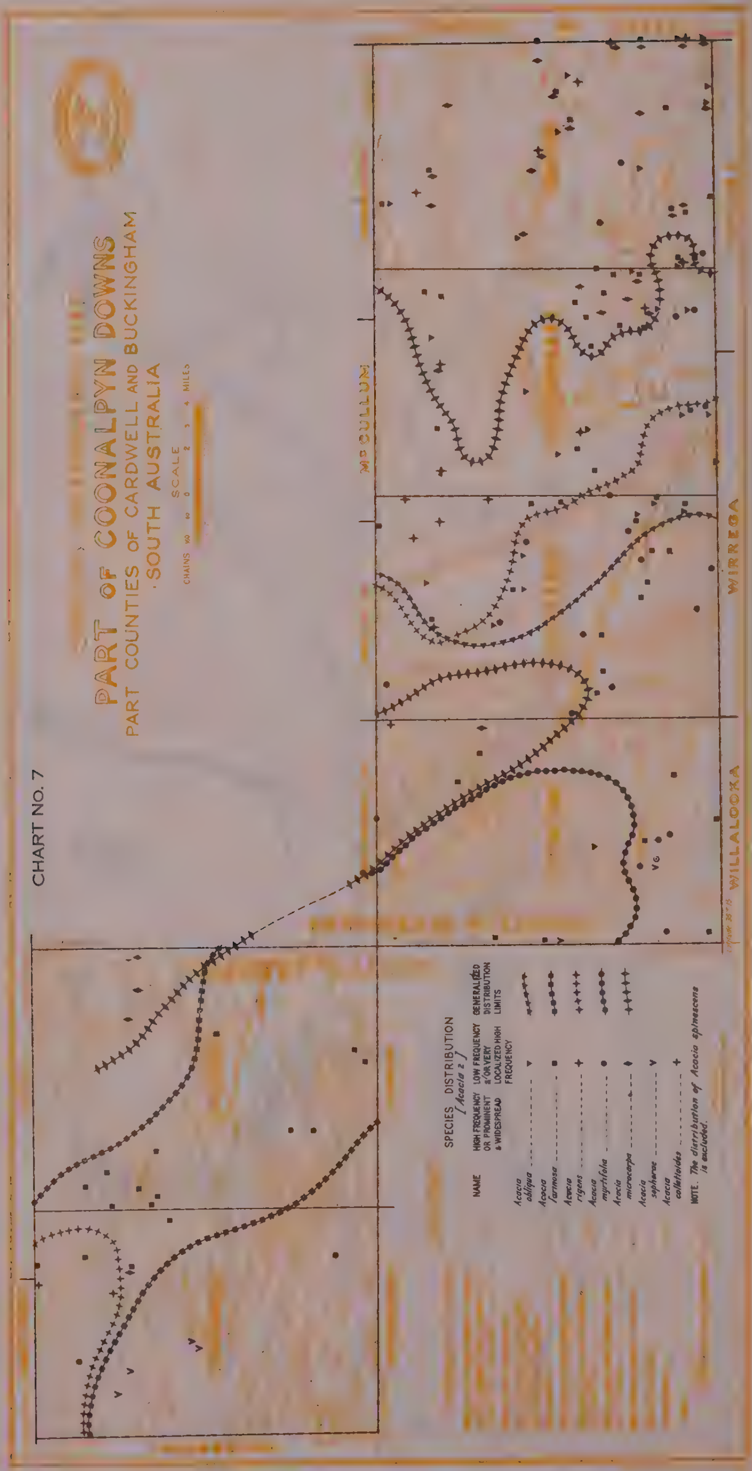


Chart No. 6.—Species distribution—*Acacia* 1.



NOTE. The distribution of *Acacia spinescens* is excluded.

Chart No. 7.—Species distribution—*Acacia* 2.

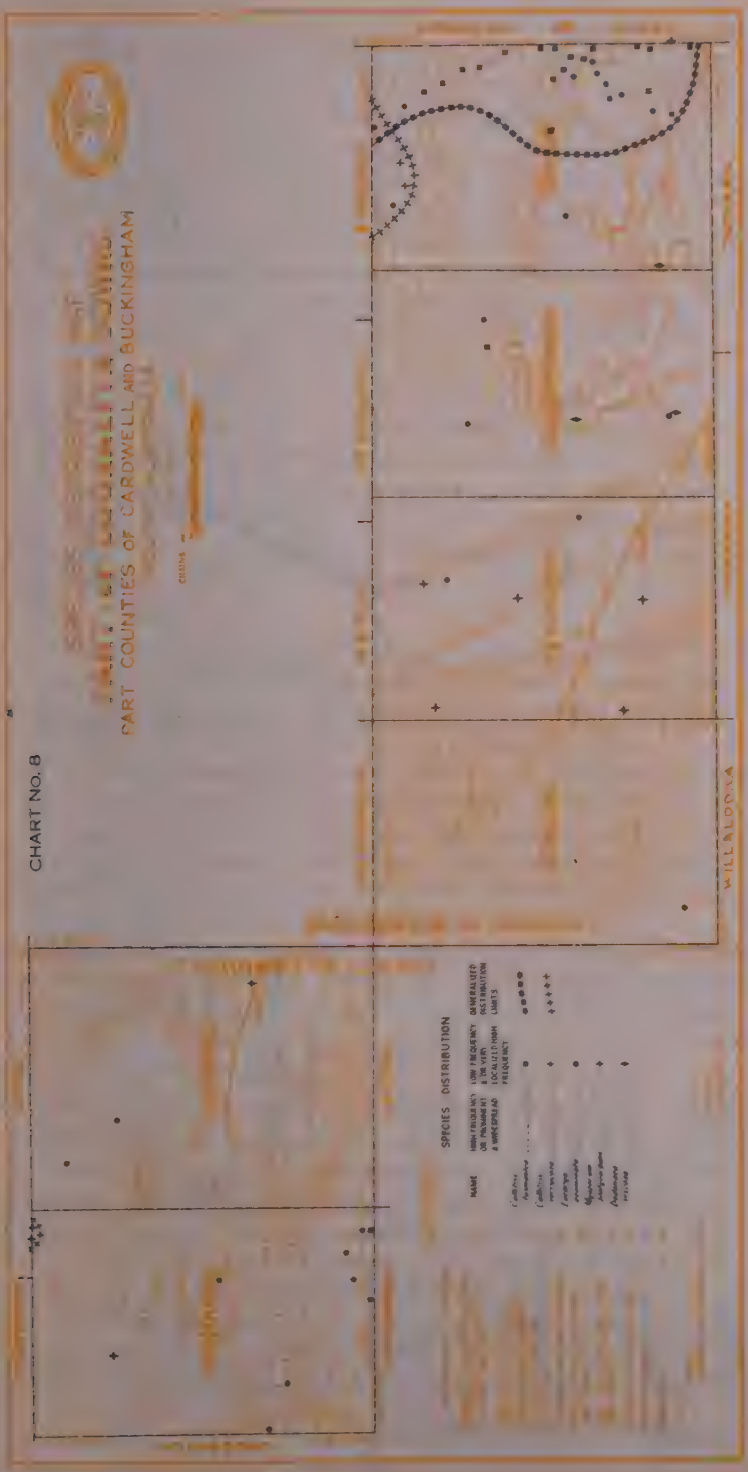


CHART No. 8
PART COUNTIES OF CARDWELL AND BUCKINGHAM
SPECIES DISTRIBUTION
NAME
HIGH FREQUENCY OR PROMINENT & WIDESPREAD
LOW FREQUENCY & OR VERY LOCALIZED HIGH FREQUENCY
GENERALIZED DISTRIBUTION LIMITS
WILLALOOKA

Chart No. 8.—Species distribution—*Callitris*, *Eucarya*, *Myoporum*, *Dodonaea*.

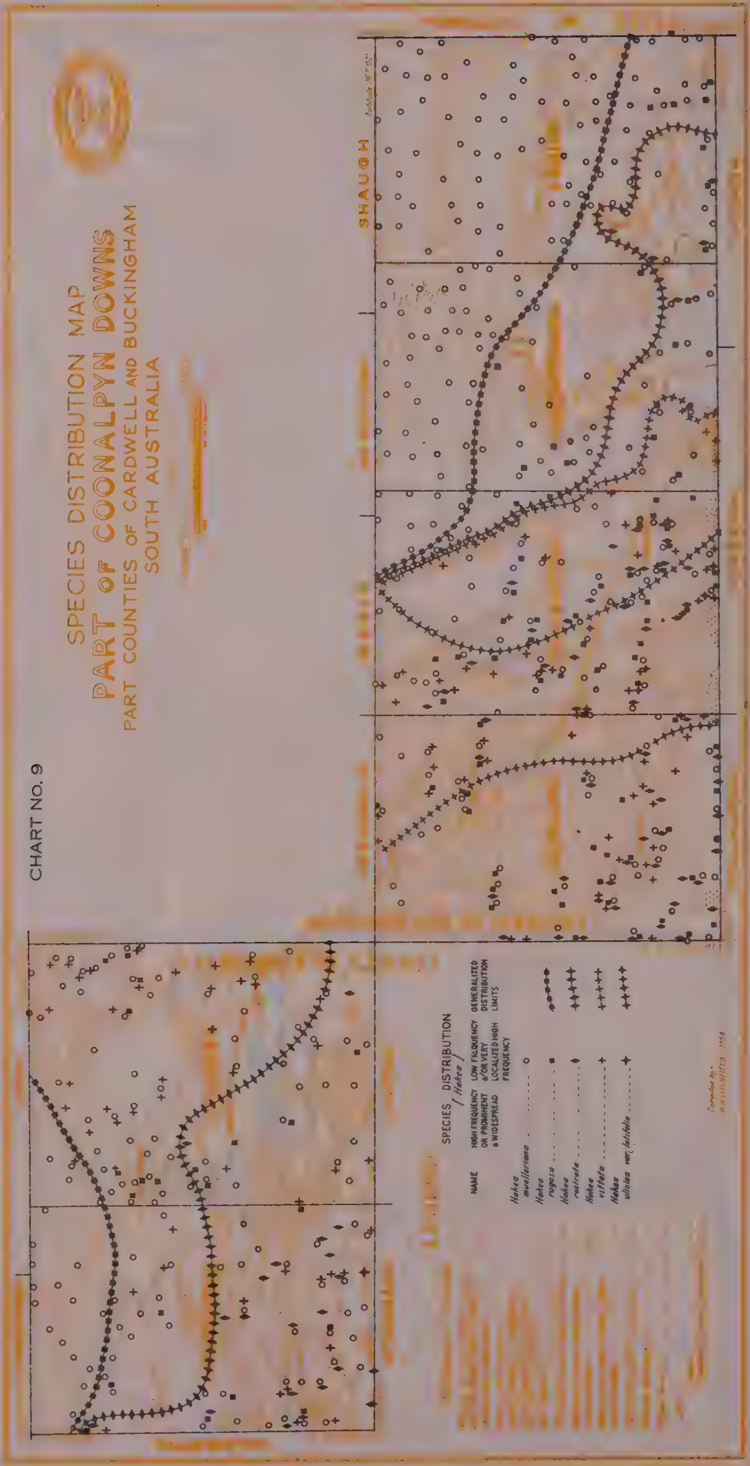


CHART NO. 9
SPECIES DISTRIBUTION MAP
PART OF COONALPYN DOWNS
PART COUNTIES OF CARDWELL AND BUCKINGHAM
SOUTH AUSTRALIA
SHAUGH
SPECIES DISTRIBUTION / Hakea /
NAME
HIGH FREQUENCY OR PROMINENT & WIDESPREAD
LOW FREQUENCY &/OR VERY LOCALIZED HIGH FREQUENCY
GENERALIZED DISTRIBUTION LIMITS
Hakea muelleriana
Hakea rugosa
Hakea rostrata
Hakea vittata
Hakea ulicina var. latifolia
Compiled by: W.H. LITCHFIELD 1954

Chart No. 9.—Species distribution—*Hakea*.

(iv) E. camaldulensis.—*E. camaldulensis* is rare in the territory and occupies only locally wet hollows and swamps where salinity is not excessive. Occasional trees or small communities occur in these situations in or near the shallow valleys in the Hundred of Cannawigara and adjacent parts of the Hundred of Senior. These occurrences represent extraneous stations relative to a wider distribution confined to watercourses and swamps in the Hundreds of Wirrega and Tatiara (Specht 1951). A series of swampy flats in the south-east corner of the Hundred of Laffer has Wirrega gilgai clay soils or allied types and supports well-grown stands of red gums. The full distribution of these flats and a similar and more extensive tract extending from the south-east side of the Hundred of Willalooka into Swedes Flats in the south-west of the Hundred of Wirrega is shown by Taylor (1933) and Specht (loc. cit.).

(v) E. baxteri.—*E. baxteri* has a wide distribution over the sand dunes of County Buckingham where it forms open stringybark-heath communities and, in a few localities, a sclerophyll woodland where the trees are larger and the spacing closer. In County Cardwell, however, the species is present only on sandhills in the southern half of the Hundreds of Richards and Coombe and the margin of area appears to follow this directional trend further west. This is surprising as stringybark occupies similar sand ridges in the Big Desert (Coaldrake 1951) where the rainfall drops as low as 13 in.

Apart from its spread over sandhills, the species has a very limited distribution on certain relatively shallow sand-sheet soils. In the eastern hundreds, these occurrences appear to be channelled into the following soil classes, namely, (1) the lime-free lateritic Berangwee soils, (2) minor occurrences of lime-free soils with siliceous hardpans, and (3) minor occurrences over soils of the Buckingham, Shaugh, and Red Bluff groups. Occupation is generally, but not invariably, associated with lime-free members of the latter types. It is thus evident that the presence of an acidic profile favours a limited competition against mallee, broombush, and heath species in this area. A very limited distribution of a stunted form on sandplain soils in the southern parts of the Downs contrasts with the above edaphic range by being associated with relatively deep members of the Laffer and Kumorna soils which have calcareous substrata. Such occurrences are reported by Taylor (1933) as occurring mainly at the southern end of the Hundred of Willalooka. Very occasional stations with similar habitats were recorded at the southern end of the Hundreds of Stirling and Pendleton.

The greater portion of growth on sandhills has a depauperate habit of the mallee type and rarely reaches more than about 20 ft in height. Areas do occur, however, where development has proceeded into a moderate-sized tree. A few such occurrences can be definitely associated with locally superior water supplies near the base of the sandy rises (for example, near Harding's Spring), and it is thus surmised that normal development of the tree is permitted where locally increased water supplies are found near the base-level of sandhills. The main centres of frequency of sclerophyll woodland occur over sandhills on the floor and margins of the shallow valleys in the southern part of the Hundred of Cannawigara and nearby areas. The combination of an alternation of blue gum flat and stringybark rise in this area thus repeats the same sequence found in many parts of the "Bangham scrub" between Bordertown and Naracoorte.

(vi) E. calcicultrix *and* E. odorata *var.* angustifolia.—Specht (1951) has referred to the difficulties encountered in identifying these two species in the Tatiara district and these are repeated in this territory. On the western side an apparent gradation in types between *E. calcicultrix* and *E. leucoxylon* creates an additional problem. Three fairly distinct ecotypes are evident in the field and these are discussed as separate entities. The reliability of species identification in these categories is limited to the representativeness of the few specimens brought in for identification.

(1) Tall mallees or trees with a semi-mallee habit with a typical "peppermint" or box-like rough bark, equiv. *E. odorata* var. *angustifolia*. The main centres of frequency are (A) over the upper slopes of Mt. Monster in the Hundred of Stirling, (B) a few stations on Keith and Coombe soils on the east side of the blue gum woodland along the margin of the ranges in the Hundred of Stirling, and (C) along the fringes of the blue gum-bull oak woodland with Wirrega soils south of Wirrega. In each case, soil fertility is probably of a higher order than in most of the sclerophyllous communities. Water relations in each case are also likely to be somewhat inferior to those of adjacent blue gum communities. Such community changes thus approach the typical differentiation in South Australia of *E. odorata*, *E. leucoxylon*, and sclerophyllous communities in response to edaphic and climatic controls. Occasional stations, usually of single trees, or a few at most, penetrate the pink gum woodlands on the west side of the Hundred of Stirling and the blue gum woodlands in the shallow valleys of the Hundred of Cannawigara.

(2) Small to moderate-sized smooth-barked mallees, equiv. *E. odorata* var. *angustifolia*. These mallees have a wide distribution with a low density east of the Hundred of Pendleton at stations which are often wet spots and poorly drained areas. Typical habitats include hollows in range corridors, ill-drained sandplain with mallee-broombush and gilgai areas with fringing locations in mallee scrub. Specht (1951) only recorded this ecotype (referred to as *E. calcicultrix*, p. 101) in the northern part of the Hundred of Tatiara on the southern fringes of the mallee communities.

(3) Small to moderate-sized mallee and semi-mallee varying from rough-barks to intermediates to a smooth-barked form equiv. *E. calcicultrix*. The distribution is centred mainly over Coombe soils with free to excessive drainage in a belt extending from the north of the Hundred of Stirling to Richards. The main centre of frequency is over the north-eastern fringes of the Keith plain. In this area and also on similarly placed habitats in the Hundred of Coombe, substrata are often porous marl or rubble and water-tables are deeper than in nearby woodlands.

(vii) E. incrassata (*including* E. angulosa).—Although *E. incrassata* is the predominant mallee of the territory, its margin of area to the south appears to lie not much further south than Willalooka and adjacent hundreds. This distribution represents part of an extensive area spread largely over light-textured soils extending from western and north-western Victoria (Zimmer 1946) to the Murray lands (Jessup 1946) and with further disjunctions through the Mt. Lofty Ranges and Kangaroo Island (Wood 1938; Northcote, unpublished data) to Eyre's Peninsula

(Crocker 1946*a*) and the mallee zone of southern coastal Western Australia (Poutsma 1953).

It is evident that the species in this territory, as elsewhere, has a strongly held occupation of wide tracts of sandy solodic soils, such as the Buckingham and Red Bluff soils, with leached topsoil sands over tight clay subsoils with poor infiltration capacities. It should therefore be tolerant to both seasonal waterlogging and summer desiccation. In addition to its occurrences under these conditions and on marginal soils with deeper sandy topsoils, such as the Shaugh group, the species has a wide but discontinuous spread over sand dunes. As Coaldrake (1951) points out, moderate-sized mallee rarely occupies the upper parts of high dunes, although mallee-heath with close spacing sometimes completely covers the lower ones. On the other hand, in a broad belt referred to previously in the western side of the Downs and at least in parts of the northern portion, very stunted mallees dominated by this species may occupy and indeed are in places concentrated on the higher dunes. It is the chief mallee species to enter *Melaleuca fasciculiflora* communities on saline sandplain.

E. incrassata extends into a number of other communities associated with soils with free to excessive drainage, the more important being the mallee scrub on Culburra soils and local developments of mallee-heaths in "ranges" on sands of moderate depth over travertine or clay. Densities are usually low on well-drained Laffer sandplain soils where the species is represented only in small areas of mallee-heath and in a sparse distribution through the sclerophyll woodlands. Around the gilgais in the eastern hundreds frequencies of this species diminish and its place is taken by other mallee species.

(viii) E. leptophylla.—*E. leptophylla* is a species sharing a similar edaphic range and widespread coexistence with *E. incrassata*. It usually has an appreciably lower density, and rarely reaches the status of a dominant or co-dominant species in mallee-heath and mallee-broombush vegetation. The species likewise has a wide continental distribution extending from subcoastal southern Western Australia to Central Western New South Wales (Beadle 1948; Black 1952; Poutsma 1953; and others).

In habitats which provide obvious stresses for eucalypt occupation, stations of this species tend to be aggregated more than coexisting mallee eucalypts into low spots such as swales between high dunes. In the eastern part of the Hundred of Coombe and a few other localized stations elsewhere in County Cardwell, the species reaches a high frequency in stunted scrub formations existing on poorly developed Coombe soils occurring on fossiliferous lime pans and marl which presumably indicate former lacustrine deposits. Coaldrake (1951) has recorded two small areas of a similar relatively dense occupation a little further east at the southern end of the Hundred of Makin.

(ix) E. diversifolia.—A marked feature of the distribution of this mallee is that its inland margin of area is sharply defined by the innermost "range" remnants and adjacent travertine sandplains. This distribution is part of its spread as a "coastal mallee" extending from Eyre's Peninsula to near Portland, Vic. (Black 1952; and others).

The edaphic range of the species shows that it is tolerant of excessively drained situations, and Coaldrake (1951) assumes it to have the lowest water status of the communities he discusses. It is entirely absent from poorly drained habitats. The densest centres of frequency are represented by sharply defined mallee scrubs on the skeletal stony soils of the ranges. On travertine plains stations are similarly often localized on to skeletal and other very shallow calcareous soils. These are often found on small hummocks on the plain.

A peculiar feature of the distribution is variation in the extent to which the species occupies sand dunes. In the eastern hundreds, occupation rarely extends beyond deep sands superimposed on the ranges. In the western hundreds and eastwards towards the Coorong and Murray Lakes (Jessup 1946), however, there is a wide zone of coexistence with *E. incrassata* on the inter-range sand ridges where both occur in a stunted form. The most easterly inter-range occurrences on sand ridges were recorded near the north-west corner of the Hundred of Pendleton.

(x) E. oleosa *and* E. gracilis.—Margins of area for these two species closely correspond except for outlying stations. This is in keeping with their wide but almost identical general distribution in the mallee zones of southern and south-western Australia as shown by Crocker and Wood (1947).

The recorded distribution is the southern fringe of an extensive area spread over the Murray lands and their margin of area indicates the upper rainfall limit for these species in this region. It lies mainly between the 18 and 19 in. isohyets.

Stations tend to follow soils which are freely to excessively drained but which are not wholly or partly occupied by heath vegetation. The main centre of frequency lies in the mallee scrub with Culburra soils where soil conditions are closer in morphology to the mallee soils of the Murray lands than elsewhere. Scattered stations are found in the adjacent ranges and occasional ones on nearby Coombe and Laffer soils. The isolated outliers recorded in the eastern hundreds occur in mallee-broombush or mallee scrub on incipiently gilgaied soils. An isolated recording of *E. oleosa* was made in mallee-heath on a low sand rise in the western side of the Hundred of Cannawigara. It is apparent that the two species are not necessarily associated with sandy soils as in western New South Wales (Beadle 1948).

(xi) E. anceps.—The distribution of *E. anceps* is distinguished from that of *E. oleosa* and *E. gracilis* by its extension from the drier mallee scrubs of the Murray lands and the Culburra soils into the mallee scrubs associated with gilgai and fringing soils of the Senior and Cannawigara groups and Buckingham soils with thin topsoils in the eastern hundreds and adjacent Victoria. There is similarly a wide continental distribution extending westwards to the mallee zone of Western Australia. The superficial "jump" in the species' edaphic range from the excessively drained Culburra soils to the poorly drained heavy gilgai soils and associated claypan types with thin topsoils is suggestive of moisture stress in the latter during the seasonal drought. Salinity levels are appreciable in the subsoil of these types and would tend to add to osmotic stresses.

(xii) E. rugosa.—The species occurs mainly amongst the range formations and, like *E. diversifolia*, has a margin of area corresponding with the easternmost ranges. The distribution extends north-westwards of the territory into the Murray lands and enters the mallee scrub on the Culburra soils. Thus, in general, the species distribution follows highly calcareous soils with low water relations which do not waterlog for long periods. It does, however, often occupy the wetter micro-habitats on the limestone hills as slight hollows, and locally deeper clay pockets than adjacent skeletal types where *E. diversifolia* is very thick. In poorly drained parts of range corridors it may be replaced by *E. anceps* and, in some cases, it appears to hybridize with the latter.

(xiii) E. behriana.—The species occurs widely around gilgais in the eastern hundreds but generally has a lower density of occurrence than *E. anceps*. Unlike the mallee species discussed previously, the main part of the species area appears to lie to the north-east of the territory in the direction of north-west Victoria (Zimmer 1946) and western New South Wales (Beadle 1948). Occurrences have, however, been recorded as far west as the South Australian highlands and adjacent mallee scrubs (Black 1952).

A few recordings were made of stations on a variant of the Buckingham soils with a thin topsoil over a red clay found on some hillsides in the shallow valleys near Cannawigara. A small outlying area also occurs in mallee broombush and the fringes of the blue gum-bull oak woodland near Wirrega.

The occurrence of the species on heavy gilgai clay soils contrasts with the species' close affinities with sandy soils in western New South Wales mentioned by Beadle.

(xiv) E. calycogona.—Although the species apparently has a wide continental distribution westwards of the territory, the distribution recorded in the eastern hundreds is apparently the south-eastern side of a species area extending northwards to the northern fringes of the Coonalpyn Downs (Coaldrake 1951) and north-western Victoria (Zimmer 1946). Stations are closely associated with the gilgai soils. The density of occurrence is generally low.

(*b*) Melaleuca (*Chart* 4)

Melaleuca spp. are widely distributed and the prevalence of this genus in the territory, as elsewhere in the greater part of Australia, is largely associated with land types which waterlog for appreciable periods. Certain species, as *M. uncinata*, are also tolerant of seasonal desiccation. Only one species, *M. pubescens*, has the greater part of its distribution on freely to excessively drained soils. Most species are known to have wide salinity tolerances.

(i) M. uncinata.—The species has a widely held occupation of the solodic and solonetzic sand-sheet soils with tight clay subsoils under 2-20 in. of sand (cf. the Buckingham, Red Bluff, and Cannawigara groups). The spacing is generally close in mallee-broombush communities but some communities show a very dense spacing where the mallees may be sparse or almost excluded. Although most of these soils are on sandplain, hillside occurrences are met with on Red Bluff soils and on some Buckingham soils or variants over some of the valley sides mainly in the Hundred of Cannawigara and certain "range" slopes where an appreciable depth of clay has accumulated.

The continental distribution of the species is very wide. The edaphic affinity of the species for degraded soils with tight claypans—many of which are solodic—is apparent both in south-western and south-eastern parts of the continent.

In this area, populations, usually of low density, extend into a number of other communities associated with other soils, namely,

(1) occasional occupation of the lower and mid slopes of sand dunes with many feet of sand (and with very occasional stations reaching the crests of such dunes);

(2) sparse occurrences in sclerophyll woodland on Laffer soils;

(3) sparse occurrences in mallee scrub on Culburra soils;

(4) a few dense communities on near-saline sandplain with firm clay subsoils (cf. the soils of the Calgara association (Jackson and Litchfield 1954)) and occasionally on adjacent heavy-textured saline soils.

(ii) M. fasciculiflora.—Plants placed under *M. fasciculiflora* have recently been divided by Black (1952) into two species, namely, *M. oraria* J. M. Black and *M. neglecta* Ewart & Wood. As no distinctions were made during the field work, the earlier arrangement is maintained here.

M. fasciculiflora usually reaches a high frequency and is a lone dominant on much of the saline and seasonally waterlogged sandplain occupied by Monkoora soils in the southern parts of the Hundreds of Richards and Coombe. This community occurs widely under similar conditions nearer the Coorong and south-westwards through the Hundreds of Laffer and McNamara as far as the north-western hundreds in County Macdonnell (Taylor 1933; and Blackburn 1952). The relative tolerances of *M. halmaturorum* and *M. fasiciculiflora* to high salinity and/or very poor drainage in these areas is apparent from their sharply defined fringing distributions around some of the salt-marshes or salt lakes with adjacent sand rises. *M. halmaturorum* forms an inner band and *M. fasiciculiflora* an intermediate one between the former and mallee-heath or woodland on the rising slope.

Sparse populations spread on to soils with improved drainage status which are occupied largely by other communities. This extends the margin of area considerable distances beyond the zone with saline sandplains. Scattered plants occur throughout most of the mallee-broombush communities on Buckingham soils and sclerophyll woodlands on the more hydromorphic members of the Laffer group. Occurrences on deeper sands with mallee-heath vegetation are rare. Localized dense communities, usually also supporting *Eucalyptus leucoxylon*, appear in a few wet hollows with Buckingham soils in the eastern hundreds. Salt sampling in these locations indicated that their salinity status lies within the range normally encountered in Buckingham soils (see Appendix II).

(iii) M. pubescens (*including* M. acuminata).—The two species can be very close in appearance and were not distinguished. *M. acuminata* has been identified only in woodlands and mallee-broombush in the Hundred of Pendleton by Coaldrake (1951). The two species are, however, known to coexist in mallee scrub elsewhere (Jessup 1946).

Life form varies from shrubs in mallee scrub and mallee-broombush to small trees under 20 ft high in savannah woodland. The tree form occurs with sparse spacing (probably somewhat closer in the virgin state) in savannah woodland on Keith soils. This woodland (blue gum–tea-tree) also occupies some low "range" hillocks with skeletal or terra rossa soils. Other localized stations, for example, low lunette banks against a saline swamp in the east side of the Hundred of Laffer, are rather similar. Such an occupation occurs elsewhere in the south-east, and on York and Eyre's Peninsulas (Crocker 1944, 1946*a*; Blackburn 1952; and others). As Crocker points out, the edaphic relations of open woodland communities on range formations dominated in various vegetation type-combinations of *Eucalyptus leucoxylon*, *M. pubescens*, and *Casuarina stricta* are sometimes very similar to those of the *E. diversifolia* scrubs. In this area, the latter are mainly found on more markedly skeletal soils and up-slope locations. A shrub-form ecotype does, however, occur in many of these mallee communities. The shrub form also usually has a moderately close spacing in the other mallee scrubs of the area, as in the scrub of mixed species on the Culburra soils and in the *E. anceps* association around the gilgais in the eastern hundreds. Extraneous stations spread out from such centres into communities such as mallee-broombush.

Local centres of frequency occur in a number of other environments and plant communities. Small woodland communities with tall shrubs and small trees, for example, the *E. fasciculosa*-*M. pubescens* type described by Coaldrake, are scattered through low spots in the inter-range corridors and some swale situations with Buckingham, Laffer, and other more calcimorphic soils. Denser communities of tea-tree alone may occupy semi-swamp and salinized grey calcareous soils in the Tintinara area. A few stations stand on the brink of samphire salt-marsh. In such localities the species appears to be exerting a tolerance towards waterlogging and high salinity of a similar order to that commonly shown by *M. halmaturorum*.

These tea-trees have a very wide range both in regard to the water relations of supporting soils and to establishment in diverse communities. A common factor in all recordings of associated soils, which may be of significance, is alkalinity and the presence of free lime in either the profile or the substratum.

(iv) M. wilsonii.—The distribution has a close association for poorly drained soils supporting mallee communities. Centres of frequency, represented by a sparse to moderate spacing amongst mallee and broombush, occur on Cannawigara soils near gilgais and the shallower topsoil variants of the Buckingham group with less than 6 in. of sand. Stations sometimes extend to gilgai depressions and occasionally deeper Buckingham soils.

(v) M. gibbosa.—The species is represented only in broombush-sedge societies in poorly drained flats and swales with Buckingham soils in the south-west corner of the Hundred of Stirling. These are probably extraneous stations of a species area extending south-westwards toward the coast and the heaths of the lower south-east (Crocker 1944; Blackburn 1952). The habitats of the species elsewhere indicate tolerance towards high water-tables. Falling rainfall associated with lengthening of the seasonal drought and/or lower water-tables apparently determine margins of area here. Coexistence with *M. fasciculiflora*, noted by Blackburn near Kingston, was not recorded.

(vi) M. halmaturorum.—As elsewhere in both littoral and inland areas, the species is closely associated with highly saline habitats with shallow seasonal water-tables. It often makes a dense fringing low forest or tall scrub around salt-marshes and salt lakes in County Cardwell. Entry on to the marsh floor probably indicates slightly improved drainage.

(*c*) Callistemon rugulosus

The edaphic range and most of the species area are close to that of the smooth-barked mallee ecotype of *E. odorata* var. *angustifolia* and the species occurs mainly in wet spots in woodland, in mallee broombush, and around gilgais. There are very few stations in the Hundreds of Stirling, Coombe, and Richards.

(*d*) Leptospermum (*Chart* 5)

The distinctive regional areas and location of stations of the three species suggest that each has contrasting water relations, in spite of partial edaphic tolerances and community relationships in common, i.e. centres of frequency of each are usually associated with heath communities or heath elements in other communities on aeolian sands. *L. myrsinoides* under these conditions is well adapted to the climatic range in the territory; *L. coriaceum* is regarded as an indicator of xeric conditions while *L. juniperinum* is associated with mesic ones.

(i) L. myrsinoides.—The species has a wide distribution in heath, mallee-heath, stringybark-heath and sclerophyll woodland and amongst the heath elements in other communities. The northerly margin of area is not known to the author but does not extend inland on sand as far as north-west Victoria (Zimmer 1946).

(ii) L. coriaceum.—The species area contrasts with *L. myrsinoides* by having only its southern margin in the territory. The main centres are on high sand ridges and sandy slopes of the ranges in the north-east of the Hundred of Coombe and the north of the Hundreds of Stirling and Pendleton. Stations are few on the sand-hills of the eastern hundreds but become more frequent to the north in the Hundred of Shaugh and County Weeah (Vic.) where rainfall is believed to decrease. The species thus mainly occupies local arid habitats at the upper end of its rainfall range.

(iii) L. juniperinum (*formerly* L. scoparium).—Occurrences are mainly restricted to heath in the southern parts of the Hundreds of Richards and Coombe which is underlain by relatively shallow water-tables. A few stations are also found amongst broombush and sedges in the south-western corner of the Hundred of Stirling where it coexists with other mesic indicators such as *Melaleuca gibbosa* and *Darwinia micropetala*. Such species are more prominent in the wetter heath lands of the lower south-east (Crocker 1944).

(*e*) Acacia (*Charts* 6 *and* 7)

The majority of species have the greater part of their area in drier environments that that of this territory. Of the 16 species recorded, 10 are reported in an ecological survey of the far north-west of Victoria (Zimmer 1946) and 13 from the areas adjacent to the Murray Lakes (Jessup 1946), but only 3 from the lower south-east (Crocker 1944) and 6 from the central Mt. Lofty Ranges (Specht and Perry 1948). Eight species have centres of frequency in woodland communities and the remainder occur mostly in mallee communities.

(i) A. pycnantha.—The adaptability of the species to occupy a position in communities other than woodland is demonstrated by its distribution here. Occurrences are found through some of the *Eucalyptus diversifolia* scrubs on limestone hills and on saline sandplain with *Melaleuca fasciculiflora* in addition to scattered stations through many woodland communities. There is no entry into mallee-broombush (*M. uncinata*) communities and stations on deep sands are rare. Certain stations in stringybark-heath have been identified as the sites of former aboriginal activity.

(ii) A. hakeoides.—Most centres of frequency are amongst woodlands—particularly in the Hundred of Pendleton where dense societies occur in some of the range corridors. A few stations were also recorded in the mallee scrub on Culburra soils and other mallee communities.

(iii) A. ligulata.—The species occurs mostly in woodland and usually shows an affinity for sandy soils with free drainage and some sort of marly or travertine substratum. The easterly margin of area corresponds with the most easterly travertine sandplain in the Hundred of Cannawigara. Occurrences in mallee-broombush are rare.

(iv) A. armata.—Stations are restricted to the skeletal soils amongst granite outcrops on Mt. Monster, and occasional ones which have spread into the adjacent *Eucalyptus fasciculosa* woodland on Laffer soil. Aboriginals collected rock for weapons here and could well have brought the seed in.

(v) A. rupicola.—The species was recorded only on shallow range soils amongst *Eucalyptus diversifolia* scrub at the northern end of the Hundred of Stirling and adjacent parts of the Hundred of Archibald.

(vi) A. dodonaeifolia.—The species was only recorded in woodland near habitations at Keith, Emu Flat, and an isolated station some miles south of Keith. It is likely that it has been introduced since settlement.

(vii) A. brachybotrya.—The species shows an affinity for moderately or freely drained sandy soils of the Buckingham and Berangwee groups amongst the woodlands in or adjacent to the shallow valleys in the Hundreds of Cannawigara and Senior.

(viii) A. calamifolia.—Extraneous occurrences are represented by stations amongst *E. leucoxylon* in gullies in hills near Red Bluff Hill, in the north-eastern side of the Hundred of Shaugh and adjacent Victoria, and several miles to the south at the "Pannikan" soak. The species is known to be widely distributed to the north-east and north-west of the Coonalpyn Downs.

(ix) A. obliqua.—The species has an affinity for the poorly drained soils of the Senior, Cannawigara, and Wirrega groups and sometimes the Buckingham soils with relatively shallow sandy topsoils. Stations on travertine sandplain are rare.

(x) A. farinosa.—The species generally has a low density distribution through the mallee communities on poorly drained soils. Stations are also found in some of the woodlands and heaths of Laffer soils and in the mallee scrub on Culburra soils. It is another case with at least a superficial jump in its edaphic range.

(xi) A. rigens.—Its distribution is mainly in mallee-broombush on Buckingham soils in the eastern hundreds, particularly Pendleton. Occasional stations are found also in the mallee scrub on Culburra soils.

(xii) A. myrtifolia.—This species has affinities for two kinds of habitat, namely, (1) sporadic occurrences, mostly amongst stringybark-heath, on the deep sands of the sandhills and (2) sporadic centres on stony parts of the ranges and stony hummocks in travertine sandplain with *Eucalyptus diversifolia* scrub.

(xiii) A. microcarpa.—This species also shows the edaphic jump in its distribution, like *Eucalyptus anceps* and others, namely, from centres in mallee scrub around the gilgais in the eastern hundreds to shallow range soils in the Hundreds of Coombe and Stirling.

(xiv) A. sophorae (*syn.* A. longifolia *var.* sophorae).—Odd stations are found on sandy soils in the coastal sides of the Hundreds of Richards and Stirling. It is probable that these stations and likewise those of *Olearia axillaris* are the result of volunteer establishment from littoral sources.

(xv) A. colletioides.—Only one centre was recorded amongst mallee-broombush on gilgai soils in the north-east part of the Hundred of Stirling. The species is known to occur through mallee communities to the north-west and the north-east of the Downs.

(xvi) A. spinescens.—The species occurs widely through the mallee communities and sparsely in the woodlands. Stations coexist with heath elements in some communities.

(*f*) Casuarina (*Chart* 5)

The tree species, *C. stricta* and *C. luehmanni* have limited distributions centred in savannah woodland; the shrubs, *C. pusilla*, *C. muelleriana*, and *C. paludosa* are widely distributed in the heaths and other sclerophyllous communities.

(i) C. stricta.—*C. stricta* has a sparse spacing through the *Eucalyptus leucoxylon-Melaleuca pubescens* woodlands on Keith soils and adjacent relatively open *E. fasciculosa* woodlands on Laffer soils. Few stations are established in nearby mallee communities. The occurrence of the species on rocky and skeletal soils is widespread in the woodlands of southern Australia and the granite outcrops provide such a habitat. Isolated stations were also recorded near two soaks far removed from any savannah area; one (Harding's Spring) at least was an aboriginal encampment.

(ii) C. luehmanni.—The species is co-dominant with *Eucalyptus leucoxylon* on the Wirrega gilgai soils south of Wirrega. This area and other isolated stations amongst *E. leucoxylon* and *E. camaldulensis* in seasonal swamps in the Hundreds of Cannawigara and Senior are extraneous to a wide area through the savannah woodlands of the Tatiara and Wimmera districts (Specht 1951).

(iii) C. pusilla *and* C. muelleriana.—The two species frequently coexist in heath and among the heath elements of other communities. *C. pusilla* is virtually ubiquitous in heath vegetation although spacing varies from rare to dense in heaths both on deep sands and Laffer soils. *C. muelleriana* is often more prominent than *C. pusilla* in stringybark-heath, mallee-heath, the more open *E. diversifolia* scrubs and adjacent mallee-heath in ranges, and mallee scrub on Culburra soils. It is usually sparsely spaced or absent from open heath except for some localized dense communities on Laffer soils. Both species may enter sclerophyllous woodland communities.

(iv) C. paludosa.—Stations in the main area generally have an affinity for travertine sandplain and particularly the more mesic areas. In this area stations on deep sands are sparsely spaced. Isolated outlying areas were, however, recorded in the eastern hundreds, namely, (1) in heath on siliceous hardpan and associated sandplain soils in Cannawigara and (2) on high sand ridges in Shaugh.

(*g*) Callitris (*Chart* 8)

Only two species, *C. tasmanica* and *C. verrucosa* occur in the Coonalpyn Downs area as such although remnants of an area of a *Callitris* (*C. propinqua* (?)) on sandy soils extends westwards from the Wimmera district to the southern fringes of the mallee communities in the north-eastern side of the Hundred of Tatiara.

(i) C. tasmanica.—Centres of frequency, some with locally dense spacing, are found on the Red Bluff soils and particularly the deeper sands cresting the hills with these soils in the eastern side of the Hundred of Senior. The distribution has also spread along many tracks in this border area and the establishment of these tracks has obviously favoured a spread in area. The latter occurrences are found mainly in stringybark-heath and mallee-heath but rarely mallee-broombush.

(ii) C. verrucosa.—The species area is centred in the continental side of the Downs and extends northwards through the mallee belts of the Murray lands and western New South Wales (Zimmer 1946; Beadle 1948; Black 1948). It is known to have a general affinity for sandy soils throughout this zone. Although Coaldrake's (1951) "*Callitris*-yacca" line probably marks off the southern limits of common occurrence, extraneous stations and absolute margins of area come many miles further south and south-westwards in places.

(*h*) Hakea (*Chart* 9)

The five species all have distributions centred in the sclerophyllous communities. The greater part of that of *H. rugosa* and *H. rostrata* lies over relatively mesic habitats and that of *H. ulicina* var. *latifolia* is spread over xeric ones.

(i) H. muelleriana.—The species has a wide range of tolerance towards sandy soils of varying physical characteristics. It is virtually ubiquitous in mallee-broombush where it occurs with a moderately wide or wide spacing. Stations extend through many communities with heath elements, but more sporadically, and can be found in both open heath and woodland and mallee formations. In localized areas, it reaches a moderately close spacing on saline sandplain. The distribution extends through the mallee scrub on Culburra and Coombe soils.

(ii) H. rugosa *and* H. rostrata.—The two species commonly coexist and their continental margins of area appear to be fairly close. Centres are most frequent in the inter-range sandplain soils on both travertine and claybeds in *Eucalyptus fasciculosa* woodland, mallee-broombush, and more sparsely in heath. Where micro-habitats vary locally, *H. rugosa* often occupies a more mesic position than *H. rostrata*. *H. rostrata* is more common on the deeper sands than *H. rugosa* but does not reach the mid or upper slopes of sand dunes. Both have a sparse distribution on range soils and in the valley systems of the eastern Hundreds.

(iii) H. vittata.—The species is restricted to heath and the heath elements in other communities on travertine sandplain and the *E. diversifolia* scrubs on the stony range soils. The species thus has a close affinity for the presence of travertine or some sort of lime pan. In open heath on inter-range sandplain, it can be a valuable indicator plant to denote the presence of such a substratum, which is usually found at a depth of less than 2 ft on Laffer and Coombe soils. Spacings become progressively sparse on Kumorna soils with increasing depth of sand and disappear on still deeper sands. Other smaller plants such as *Dampiera rosmarinifolia* and *Logania linifolia* appear to have a similar distribution in heath.

The species referred to by Zimmer (1946) as *H. vittata* in north-western Victoria is classified as a tree and is clearly a different ecotype from the low almost prostrate shrub found in South Australia.

(iv) H. ulicina *var.* latifolia.—Stations are usually sparse and were recorded mainly in *E. diversifolia* scrub in the Hundred of Pendleton. The species has also been recorded by Coaldrake (unpublished data) on high sand ridges further north in the Hundreds of Makin and McCallum, and one such station was found in the Hundred of Richards.

(*i*) Eucarya acuminata (*Chart* 8)

The species has a very sporadic geographical and edaphic range of stations and can occur on most moderate to well-drained sandy soils irrespective of the established community. The only area where it is consistently met with is in shrub form in heath in the south-western side of the Hundred of Senior. In the Hundred of Richards, the crest of high sand ridges is a favoured site. Other authors have suggested that birds, in particular the emu, are important agents in seed dissemination, and this is consistent with a haphazard distribution. An ecotype, in the form of a small tree, is occasionally found in woodlands.

(*j*) Myoporum platycarpum (*Chart* 8)

The species has a wide distribution in arid Australia and it is interesting to note its presence in a moderate-rainfall zone. Stations are rare and were recorded, with one exception, in poorly drained hollows in inter-range corridors.

(*k*) Dodonaea viscosa (*Chart* 8)

A few extraneous stations of a distribution on sandy soils in the Tatiara district are found in the valleys in the Hundreds of Cannawigara and Senior.

IV. Suggestions relating to Post-arid Migrations

Crocker and Wood (1947) have discussed the probability of the wholesale destruction of vegetation in a Mid-Recent Arid Period in southern Australia and subsequent recolonization from various refuges. In the case of the Coonalpyn Downs the principal refuges postulated were the Grampians and the Mt. Lofty-Flinders Range system. There is evidence to suggest that refuges or at least vegetated areas were probably present in the region in spite of widespread sand dune formation.

Characteristics of certain of the sandplain soils suggest that they have been little influenced by deflation and hence they presumably remained vegetated. Relatively stable landform conditions at the close of the Pleistocene, coupled with moderate or high rainfall and continuous ingress of cyclic salt are likely to have been optimal conditions for maximum textural differentiation during soil formation in deposits with an appreciable content of sand. The distribution of the coarse sand-fine sand ratios derived from the mechanical analysis of three sandplain profiles placed some appreciable distance from any sand dunes was examined and two (profiles 1 and 20) show almost uniform ratios within their A and B horizons. This suggests uniform parent material at the individual sites (see Table 2).

TABLE 2

THE RATIO OF COARSE SAND TO FINE SAND IN THREE SANDPLAIN PROFILES,* COONALPYN DOWNS

	Profile 1		Profile 2		Profile 20	
Horizon	A_1	B_1	A_1	B_1	A_1	B_1
Soil No.	17213	17216	17220	17224	17336	17339
Coarse sand (%)	13	7	11	4	32	16
Fine sand (%)	81	41	82	49	63	34
Ratio, C.S./F.S.	1:6·2	1:6·0	1:7·5	1:12·2	1:2·0	1:2·1

* The location of these three profiles is shown on a Soil Association Map, Part of Coonalpyn Downs (Blackburn *et al.* 1953). The three profiles are taken from extensive sweeps of sandplain in the Hundreds of Stirling (Nos. 1 and 2) and Cannawigara (No. 20).

This raises doubt concerning the occurrence of long-distance marches by dunes formed off the sandy topsoils of the pre-existing consolidated dunes, since this should have produced sharp changes in the composition of the silica skeleton of soil horizons of an aeolian as opposed to a sedentary origin. Such marches would have engulfed and destroyed vegetation apart from the effects of climatic stress. An alternative explanation is given above for the very low percentages of silt and clay in the A horizons of sandplain soils, which is used by Crocker (1946*b*, see pp. 23 and 47) as evidence of their aeolian origin. The deeper sandy surfaces formed in the Pleistocene would have been the most unstable areas in the period of stress. These are believed to have formed not only on the "ranges" but also in belts of relatively coarse sediments through the fluviatile plain on the east side of the "ranges" (Blackburn, personal communication). These deposits could be derived either from a precursor of the Murray anastomosing in this area (Howchin 1929; Coaldrake 1951) or otherwise from local aggradation of sediments carried from a low uplifted sandstone (lateritic) peneplain, now reduced to remnants in the "Big Desert" of Victoria, at places such as Red Bluff Hill (see also Coaldrake 1954). Refuges, other than on sandplains, may have existed where there are no indications of any drastic modification to landscape or soil during the Arid Period. These include some swamps, parts of the hill and valley systems, the granite monadnocks, and loamy soils supporting savannah woodland.

As the vegetation of the territory now represent a broad transition zone between the mallee belt and the forests and woodlands of the wetter southern areas, substantial contributions to its flora are made from both zones. Numerous examples of species area extending in one or the other direction from this territory are cited in the text and similar trends could be given for many others not specifically mentioned. Advances of species from refuges or from a spread of southern elements have undoubtedly intermingled with spreading mallee scrub elements. Xeric species, such as *Myoporum platycarpum* and *Triodia irritans*, could well have arrived during the period of stress and consequently may have been pioneers during re-establishment of disturbed areas. The spread of heath during the stabilization of the sand dunes has been very extensive but some of the other species and/or community migrations, if coming from refuges, could have been relatively localized.

The distributions of a number of species only partially occupy their apparent edapho-climatic range, even near centres of frequency where pressure by competition against spreading would be minimal. The failure of *Eucalyptus fasciculosa* to occupy many travertine sandplains with heath, Laffer soils, and a similar water-table regime is a case in point. Similarly, the margins of area of *E. baxteri* and *E. viminalis* on sand ridges cannot or can only be partially correlated with edaphic or climatic factors. This suggests that the relatively short period since the Arid Period has been insufficient to stabilize completely the communities, and that some active migration still occurs. In some areas, heath may represent only a seral stage towards sclerophyll woodland as the climax vegetation.

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APPENDIX I

A LIST OF NATIVE PLANTS RECORDED DURING SOIL SURVEYS IN THE COONALPYN DOWNS WITH NOTES ON THE OCCURRENCE OF THE SMALLER PLANTS

The identifications are according to J. M. Black's "Flora of South Australia", except *Eucalyptus* (see text).

Key to Symbols: T = trees > 20 ft high; t^- = small trees, generally 10-20 ft high; S = shrubs, usually 2-10 ft high; s^- = small shrubs, usually < 2 ft high; H = herbs

Family	Species	Habit	Occurrence
Polypodiaceae	*Cheilanthes tenuifolia*	H	Restricted to skeletal soils around granite outcrops
Pinaceae	*Callitris tasmanica*	S	Common in parts (see text)
	C. verrucosa	S or t^-	" " " " "
Gramineae	*Themeda australis*	H	Occasional; on sandplain with woodlands
	Neurachne alopecuroides	H	Occasional but widespread; on sandplain and sand dunes with various sclerophyllous communities
	Stipa elegantissima	H	Restricted to savannah woodland
	S. variabilis	H	" " " "
	S. semibarbata	H	Usually occasional but density may increase markedly after firing; on sandplain and sand dunes with various sclerophyllous communities, particularly those with heath elements
	S. pubescens	H	Restricted to savannah woodland
	S. eremophila	H	Locally common; incipient gilgai soils with mallee scrub in eastern hundreds
	S. tenuiglumis	H	Restricted to savannah woodland
	Danthonia caespitosa (formerly *semiannularis*)	H	Mainly restricted to savannah woodland; occasionally in cleared or partially cleared sandplain habitats and gilgai areas
	Triodia irritans	H	Occasional to frequent; on sandplain and sand dunes; most prevalent as a heath element in northerly parts of the eastern hundreds
	Distichlis spicata	H	Occasional to locally common in the salinized zone on the coastal side
	Poa australis	H	Occasional in the salinized zone usually on salinized grey calcareous soils or saline sandplain
Cyperaceae	*Schoenus deformis*	H	Common on sandplain and sand dunes as a heath element
	Tetraria capillaris	H	Common in parts of the salinized zone, usually on saline sandplain with low broombush or sedge communities
	Scirpus nodosus	H	Locally common on disturbed sandhills around soaks and similar habitats
	Lepidosperma congestum	H	Widespread (common or frequent) on sandplain and sand dunes and various sclerophyllous communities including heath

APPENDIX I (*Continued*)

Family	Species	Habit	Occurrence
Cyperaceae (*Continued*)	*Lepidosperma viscidum*	H	Occasional; only recorded on rocky habitats
	L. carphoides	H	Widespread and common on sandplain and sand dunes; various sclerophyllous communities including heath
	Caustis pentandra	H	Occasional as a mesic heath element in moderately drained sandplain in the salinized zone
	Cladium filum	H	Locally frequent in the salinized zone; on saline sandplain and other salinized soils with broombush or sedge communities; occasional in fringing woodlands
	C. junceum	H	Locally frequent around wet spots in the salinized zone
	Gahnia deusta	H	Locally common on stony "range" situations
	G. trifida	H	Occasional as a mesic heath element in moderately drained sandplain in the salinized zone. In this area, the species was not recorded in highly salinized habitats
	G. lanigera	H	Common and widespread on the shallow calcareous soils on plains and "ranges" and some gilgai "puff" soils; in mallee scrubs and woodland
	Chorizandra enodis	H	Locally common on heavy swampy soils, including some gilgai depressions
Restionaceae	*Leptocarpus brownii*	H	Locally common in the salinized zone; on saline sandplain in broombush and sedge communities; lower densities on other sandplain soils in the central hundreds in heath, mallee-broombush, and woodlands
	Hypolaena fastigiata	H	Common and widespread on sand dunes and other deep sands as a heath element
	Lepidobolus drapetocoleus	H	,, ,, ,, ,, ,,
Centrolepidaceae	*Centrolepis polygyna*	H	Recorded only on cleared saline sandplain
	C. strigosa	H	,, ,, ,, ,, ,,
Juncaceae	*Juncus pallidus*	H	Recorded only in cleared gilgai areas
Liliaceae	*Dianella revoluta*	H	Occasional and usually on sandplain with sclerophyllous woodland
	Reya umbellata	H	Occasional but widespread on sandplain and rocky soils
	Lomandra effusa	H	Common in savannah woodland; occasional in heath
	L. glauca	H	Occasional but widespread on sandplain, sand dunes, and rocky soils; heath element

APPENDIX I (*Continued*)

Family	Species	Habit	Occurrence
Liliaceae (*Continued*)	*Lomandra juncea*	H	Occasional in heath
	L. leucocephala	H	,, ,, ,,
	Chamaescilla corymbosa	H	Occasional in mallee-broombush
	Dichopogon fimbriatus	H	Occasional in woodlands
	Xanthorrhoea semiplana and/or *X. australis*	H	Frequent in heath, extending into woodlands and mallee-broombush; on sandplain and sand dunes. This species has been recorded on soils with as little as 1-2 in. of topsoil sand
Orchidaceae	*Thelymitra aristata*	H	Occasional in mallee-broombush
	T. rubra	H	,, ,, ,,
	T. antennifera	H	,, ,, ,,
	Microtis unifolia	H	Occasional; in woodlands
	Lyperanthus nigricans	H	Common at times in mallee-broombush after firing
	Diuris maculata	H	Occasional in woodlands and mallee-broombush
Casuarinaceae	*Casuarina stricta*	t^-	Common in parts (see text)
	C. luehmanni	T	,, ,, ,, ,, ,,
	C. paludosa	S	,, ,, ,, ,, ,,
	C. pusilla	s^-	Common to frequent and widespread (see text)
	C. muelleriana	S	Common in parts (see text)
Proteaceae	*Isopogon ceratophyllus*	s^-	Occasional but widespread; in heath and among heath elements in other communities
	Adenanthos terminalis	s^-	Common in heath and among heath elements in other communities
	Conospermum patens	s^-	Occasional or locally common in heath, particularly on sand dunes
	Persoonia juniperina	S	Occasional or locally common in heath; occasional in other sclerophyllous communities
	Hakea vittata	s^-	Common in parts (see text)
	H. rostrata	S	,, ,, ,, ,, ,,
	H. rugosa	s^-	,, ,, ,, ,, ,,
	H. ulicina var. *latifolia*	S	,, ,, ,, ,, ,,
	H. muelleriana	S	,, ,, ,, ,, ,,
	Banksia marginata	S & t^-	Common or locally frequent and widespread in heath and in heath elements in other communities; more prevalent on travertine sandplain and swales than sand dune situations. The tree form occurs only in certain of the more mesic woodlands and near soaks

APPENDIX I (*Continued*)

Family	Species	Habit	Occurrence
Proteaceae (*Continued*)	*Banksia ornata*	S	Common or frequent in heath and among heath elements in other communities; more prevalent on sand dunes and deep sands on plains than travertine sandplain or swale situations
	Grevillea huegelii	s^-	Common in some woodland, mallee-broombush, and other mallee communities in the eastern hundreds
	G. ilicifolia	s^- & S	Occasional in mallee-broombush and mallee scrubs both on "ranges" and around gilgais; rarely on deeper sandy soils
	G. lavandulacea	s^-	Occasional on various sandplain soils; in various communities
Santalaceae	*Exocarpus cupressiformis*	t^-	Occasional: restricted to sandy soils with woodland in the shallow valleys of the eastern hundreds
	E. sparteus	S	Occasional in woodlands
	Leptomeria aphylla	S	Occasional in woodlands and mallee scrub
	Choretrum glomeratum	S	Common in parts: on sandplain and sand dunes with mallee or heath communities
	Eucarya acuminata	S	Common in parts (see text)
Loranthaceae	*Loranthus miquelii*		Common in parts on the eucalypts of woodlands; not recorded on mallee
Chenopodiaceae	*Atriplex semibaccata*	H	Only recorded on cleared saline sandplain
	Arthrocnemum sp.	H	Restricted to salt-marsh
Amaranthaceae	*Ptilotus macrocephalus*	H	Occasional in woodlands
Phytolaccaceae	*Gyrostemon australasicus*	s^-	Common in parts on sandplain and sand dunes; density increases along tracks
Aizoaceae	*Carpobrotus aequilaterus*	H	Occasional: in various sandplain habitats: often in disturbed situations
Ranunculaceae	*Clematis microphylla*		Occasional: climber on trees and mallees and other shrubs
Lauraceae	*Cassytha melantha*		Common in parts: climber, mainly on mallee
Droseraceae	*Drosera* spp.	H	Common in parts; in various communities
Pittosporaceae	*Bursaria spinosa*	S	Common in parts: usually a tall shrub in woodlands and stunted in the mallee scrubs around gilgais
	Cheiranthera linearis	s^-	Occasional in woodland
	Billardiera cymosa		Occasional: climber on various shrubs
Leguminosae	*Acacia armata*	S	Restricted mainly to granite outcrops (see text)
	A. obliqua	S	Common in parts (see text)
	A. microcarpa	S	” ” ” ” ”
	A. spinescens	s^-	Common and widespread (see text)
	A. dodonaeifolia	t^-	Occasional (see text)
	A. brachybotrya	S	Common in parts (see text)
	A. ligulata	S	” ” ” ” ”

APPENDIX I (*Continued*)

Family	Species	Habit	Occurrence
Leguminosae (*Continued*)	*Acacia hakeoides*	S	Common in parts (see text)
	A. myrtifolia	S	,, ,, ,, ,, ,,
	A. pycnantha	t^-	,, ,, ,, ,, ,,
	A. calamifolia	t^-	,, ,, ,, ,, ,,
	A. rupicola	s^-	,, ,, ,, ,, ,,
	A. farinosa	s^-	,, ,, ,, ,, ,,
	A. rigens	S	,, ,, ,, ,, ,,
	A. colletioides	s^-	Occasional (see text)
	A. sophorae	S	,, ,, ,,
	Gompholobium minus	s^-	Occasional; in heath on deep sands in the well-drained portions of the salinized zone
	Daviesia ulicina var. *ruscifolia*	S	Restricted to sclerophyll woodland in the shallow valleys and the Red Bluff soils with mallee-broombush of the low hill systems in the eastern hundreds
	D. genistifolia	s^-	Occasional; in swampy woodlands and gilgai fringe areas in the eastern hundreds
	D. brevifolia	s^-	Common and widespread as a heath element
	Eutaxia microphylla	s^-	Common in parts and widespread; in sandplain communities and mallee scrub around gilgais
	Pultenaea pedunculata	s^-	Common in parts and widespread in sandplain and gilgai fringe communities
	P. vestita	s^-	Restricted to saline sandplain
	P. tenuifolia	s^-	Common and widespread in sandplain communities
	P. prostrata	s^-	,, ,, ,, ,, ,,
	P. densifolia	s^-	Occasional; restricted to shallow soils supporting mallee scrub on "ranges" and limestone plain
	P. acerosa	s^-	Occasional; in sandplain communities
	Phyllota pleurandroides	s^-	Common on sandplain and sand dunes as a heath element
	Dillwynia hispida	s^-	,, ,, ,, ,, ,,
	D. floribunda	s^-	Common on sandplain; in various communities
	D. uncinata	s^-	Common in gilgai fringe areas
	Kennedya prostrata	H	Occasional; on stony and other situations
Geraniaceae	*Pelargonium inodorum*	H	Recorded only on cleared saline sandplain
Linaceae	*Linum marginale*	H	Occasional; only recorded in woodland and mallee communities in the western hundreds
Rutaceae	*Zieria veronicea*	s^-	Occasional but widespread; in heath on deep sands
	Boronia caerulescens	s^-	Common and widespread in heath

Appendix I (*Continued*)

Family	Species	Habit	Occurrence
Rutaceae (*Continued*)	*Boronia filifolia*	s^-	Common in parts; in heath
	B. inornata	s^-	Occasional; only recorded on shallow soils with mallee communities in "ranges"
	Correa rubra	s^-	Common and widespread; on sandplain and sand dunes in heath and as a heath element in other communities
	Phebalium pungens	s^-	Occasional; recorded only on sandplain with mallee-broombush
	P. brachyphyllum	s^-	Occasional; restricted to mallee scrub in the western hundreds
	P. stenophyllum	s^-	Occasional or locally common, in heath
	P. bullatum	s^-	Occasional; recorded only in heath on travertine sandplains
Polygalaceae	*Comesperma ciliatum*		Occasional; climber on various shrubs
	C. volubile		,, ,, ,, ,,
	C. calymega	s^-	Occasional; recorded only in heath in the western hundreds
	C. polygaloides	s^-	Occasional; recorded only in mallee scrub and woodlands
Euphorbiaceae	*Bertya mitchellii*	S	Occasional but widespread; on sandplain in heath, mallee, and woodland communities
Stackhousiaceae	*Stackhousia monogyna*	H	Common in parts; occurs in both sclerophyllous and savannah vegetation (two distinct ecotypes)
Sapindaceae	*Dodonaea viscosa*	S	Occasional (see text)
	D. bursariifolia	s^-	Common in mallee scrub around gilgais
	D. humilis	s^-	Occasional; in mallee scrub on shallow calcareous soils in the western hundreds
Rhamnaceae	*Pomaderris racemosa*	S	Locally common; recorded only in savannah woodland
	P. obcordata	s^-	Common on stony soils in mallee scrub on "ranges"
	Spyridium spathulatum	s^- & S	Occasional or locally common; well-grown forms restricted to granite outcrops and occasionally in mallee-broombush. A slender form was also recorded in heath in the western hundreds
	S. vexilliferum	s^-	Common in parts; recorded only in heath in travertine sandplain
	S. eriocephalum	s^-	Common in parts; prevalent on sandplain with mallee-broombush, occasionally in mallee scrub
	S. subochreatum	s^-	Common and widespread in heath; (*S.s.* var. *laxiusculum* in the western hundreds)
	Cryptandra leucophracta	s^-	Common and widespread in heath
	C. tomentosa	s^-	,, ,, ,, ,, ,,
Malvaceae	*Plagianthus microphyllus*	s^-	Restricted to salt-marsh

APPENDIX I (*Continued*)

Family	Species	Habit	Occurrence
Sterculiaceae	*Lasiopetalum behrii*	s^{-}	Common on stony soils in mallee scrub on "ranges"; also recorded on shallow soils on the Red Bluff Hill lateritic residual
	L. baueri	s^{-}	Common on sandplain with mallee-broombush and in mallee scrub around gilgais; also recorded in mallee scrub on shallow calcareous and stony soils
	Thomasia petalocalyx	s^{-}	Common on sandplain in woodlands
Dilleniaceae	*Hibbertia sericea*	s^{-}	Common and widespread on sandplain and sand dunes in various scleropyyll communities
	H. stricta	s^{-}	,, ,, ,, ,, ,,
	H. virgata var. *crassifolia*	s^{-}	,, ,, ,, ,, ,,
Violaceae	*Hybanthus floribundus*	s^{-}	Occasional; in heath
Thymelaeaceae	*Pimelea glauca*	s^{-}	Occasional; on sandplain in mallee and woodland communities
	P. stricta	s^{-}	,, ,, ,, ,, ,,
	P. flava	s^{-}	Occasional; in mallee communities in the central hundreds
	P. serpyllifolia	s^{-}	Recorded only in woodland in the shallow valleys in the Hundred of Cannawigara
	P. octophylla	s^{-}	Common in parts and widespread in heath
	P. phylicoides	s^{-}	Common on deep sands in heath
Myrtaceae	*Baeckea crassifolia*	s^{-}	Common on sandplain with mallee-broombush; enters mallee scrubs
	B. ericaea	s^{-}	Common and widespread in heath
	B. behrii	S	Common and widespread on sandplain and sand dunes; in various sclerophyll communities including heath; locally dense on well-drained slopes above wet spots
	Leptospermum coriaceum	S	Common in parts (see text)
	L. juniperinum (formerly *L. scoparium*)	S	,, ,, ,, ,,
	L. myrsinoides	S	Common and widespread (see text)
	Kunzea pomifera	s^{-}	Common in parts on sandplains with heath or woodland; density is increased by disturbance
	Callistemon rugulosus	S	Common in parts (see text)
	Melaleuca wilsonii	s^{-}	,, ,, ,, ,,
	M. gibbosa	s^{-}	Occasional (see text)
	M. halmaturorum	S or t^{-}	Common in parts (see text)
	M. pubescens	S or t^{-}	,, ,, ,, ,,
	M. uncinata	S	Frequent and widespread in parts (see text)

APPENDIX I (*Continued*)

Family	Species	Habit	Occurrence
Myrtaceae (*Continued*)	*Melaleuca fasciculiflora*	s$^-$	Frequent and widespread in parts (see text)
	Eucalyptus camaldulensis	T	Occasional (see text)
	E. diversifolia	S or t$^-$	Frequent in parts (see text)
	E. baxteri	t$^-$ or T	" " " " "
	E. viminalis	t$^-$ or T	Common in parts (see text)
	E. incrassata	S or t$^-$	Frequent and widespread (see text)
	E. anceps	t$^-$	Frequent in parts (see text)
	E. rugosa	t$^-$	Common in parts (see text)
	E. leptophylla	S or t$^-$	Common and widespread (see text)
	E. oleosa	t$^-$	Frequent in parts (see text)
	E. calycogona	t$^-$	Common in parts (see text)
	E. gracilis	t$^-$	" " " " "
	E. leucoxylon	T	Common and widespread (see text)
	E. calcicultrix	t$^-$	Common in parts (see text)
	E. odorata var. *angustifolia*	t$^-$ or T	" " " " "
	E. behriana	t$^-$	" " " " "
	E. fasciculosa	T	Frequent in parts (see text)
	Darwinia micropetala	s$^-$	Common in parts of the saline and wetter sandplains with broombush communities
	Calythrix tetragona	s$^-$	Common and widespread on sandplains in various sclerophyll communities including heath
	Lhotzkya alpestris	s$^-$	Common on sand dunes in heath
Haloragaceae	*Loudonia behrii*	H	Common in parts; on sandplain in mallee communities
Umbelliferae	*Xanthosia pusilla*	H	Occasional; in woodlands
	X. dissecta ?	H	Recorded only on cleared saline sandplain
Epacridaceae	*Styphelia exarrhena*	s$^-$	Common on sandplain and sand dunes in heath and as a heath element in other communities
	Astroloma humifusum	s$^-$	Common on sandplain in various communities including heath
	A. conostephioides	s$^-$	Common on deep sands and sand dunes in heath and as a heath element in other communities
	Lissanthe strigosa	s$^-$	Common on sandplain in various communities
	Leucopogon costatus	s$^-$	Common on deep sands and sand dunes; in heath
	L. rufus	s$^-$	Occasional; in heath and as a heath element in other communities
	L. woodsii	s$^-$	Common on deep sands and sand dunes; in heath
	L. clelandii	s$^-$	Common on sandplain in various communities
	Acrotriche serrulata	s$^-$	Common; in sclerophyll communities
	A. affinis	s$^-$	Common on sandplain in woodlands

APPENDIX I (*Continued*)

Family	Species	Habit	Occurrence
Epacridaceae (*Continued*)	*Acrotriche cordata*	s^-	Common in mallee scrub, both on shallow stony soils in "ranges" and on highly calcareous gilgai "puffs"
	Brachyloma ericoides	s^-	Common on sandplain in various communities
	B. daphnoides	S	Restricted to mallee-broombush and sclerophyll woodlands in the shallow valley and low hill systems of the eastern hundreds
	Epacris impressa	s^-	Recorded only in heath in the Hundred of Willalooka
Loganiaceae	*Logania linifolia*	s^-	Common on sandplain in various communities, particularly heath on travertine sandplain; occasional on stony "range" soils
Gentianaceae	*Villarsia* sp.	H	Occasional; in wet spots on sandplain
Borraginaceae	*Halgania cyanea*	s^-	Common on shallow calcareous soils with mallee scrub in the western hundreds
Labiatae	*Ajuga australis*	H	Common in parts of the woodlands in the shallow valleys in the Hundred of Cannawigara
	Prostanthera aspalathoides	s^-	Common in mallee scrub with gilgais and fringing sandplain in the eastern hundreds
	P. microphylla	s^-	Restricted to mallee scrub on shallow calcareous soils in the western hundreds
	Westringia angustifolia	s^-	Common in mallee scrub with gilgais and fringing sandplain in the eastern hundreds
Solanaceae	*Solanum simile*	H	Recorded only on cleared ground
Scrophulariaceae	*Euphrasia collina*	H	Common in parts; on deep sand in heath
Myoporaceae	*Myoporum platycarpum*	t^-	Occasional (see text)
Campanulaceae	*Wahlenbergia gracilis*	H	Occasional; in woodlands
Goodeniaceae	*Goodenia robusta*	H	Common in various communities
	G. varia	H	Common in parts with a prostrate habit in mallee scrub around gilgais; also recorded in mallee scrub on shallow calcareous soils. The erect form is restricted to granite outcrops
	Dampiera rosmarinifolia	s^-	Common on travertine sandplain in heath and woodland
	D. lavandulacea	s^-	Common on sandplain in various communities
Brunoniaceae	*Brunonia australis*	H	Occasional; recorded only in woodlands in the western hundreds
Stylidiaceae	*Stylidium* sp.	H	Occasional; recorded only in heath and sclerophyll woodland in the western hundreds

APPENDIX I (*Continued*)

Family	Species	Habit	Occurrence
Compositae	*Vittadinia triloba*	H	Occasional; mainly in savannah woodland
	Olearia axillaris	S	Occasional; in various communities in the western hundreds
	O. ramulosa and/or *O. floribunda*	s^-	Common in parts; usually in mallee scrub around gilgais and fringing sandplain. Occasional on shallow calcareous soils with woodland or mallee scrub
	O. lepidophylla	s^-	Common in parts; both in heath and mallee scrub
	O. glutinosa	S	Occasional; recorded only in heath on travertine sandplains
	O. picridifolia	H	Locally common; in mallee scrub around gilgais and fringing sandplain
	O. ciliata	H	Common in heath
	Erechthites quadridentata	H	Sometimes frequent in new pastures after seeding
	Senecio lautus	H	„ „ „ „ „
	Cassinia aculeata and/or *C. laevis*	S	Common in mallee scrub around gilgais and fringing sandplain
	Helichrysum obtusifolium	H	Common in heath
	H. baxteri	H	Occasional; in heath
	H. leucopsidium	H	Occasional; in woodland
	H. blandowskianum	H	Occasional; in heath and woodland
	H. scorpioides	H	„ „ „ „ „
	H. apiculatum	H	Common in parts; in savannah and sclerophyll woodlands
	H. retusum	S	Common in parts; in mallee scrubs, mainly around gilgais
	Millotia tenuifolia	H	Recorded only on granite outcrops
	Humea pholidota	S	Occasional; recorded in heath and low broombush communities
	Ixodia achilleoides	s^-	Occasional; in mallee communities
	Podolepis rugata	H	Occasional; recorded only in woodland
	Craspedia uniflora	H	Occasional; in various communities density may increase after firing
	Microseris scapigera	H	Occasional; in various communities

APPENDIX II

SALINITY LEVELS IN REPRESENTATIVES OF THE SOIL GROUPS

The soils were sampled in the spring of 1951 and of 1952

Soil Group	Maximum Salinity recorded in the Top Foot of Soil (in % total soluble salts)	Soil Group	Maximum Salinity recorded in the Upper Foot of Subsoil (in % total soluble salts)
Keith	0·03–0·05	Laffer	0·01–0·23
Culburra	0·04–0·11	Kumorna	0·05
Brimbago	0·02	Richards	0·13
Senior	0·17–0·27	Shaugh	0·04–0·11
Wirrega	0·44	Colebatch	0·02
Willyama	0·06	Buckingham	0·04–0·46
Lake Ellen*	0·10–1·0	Red Bluff	0·05–0·23
		Cannawigara	0·43–0·57
		Monkoora	0·33–0·62

* Excluding surface incrustations in these soils.

THE MORPHOLOGY OF RED BEET (*BETA VULGARIS* L.) MITOCHONDRIA

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Summary

The morphology of mitochondria extracted from beet (*Beta vulgaris* L.) tissue was examined by phase contrast and electron microscopy and compared with the structure of mitochondria in tissue sections. The structure of the beet mitochondria proved much more labile than that of animal mitochondria and no really satisfactory way of preserving it was found. However, it was demonstrated that the organelles, which were either spherical or ovoid, were bounded by typical double membranes, presumably lipo-protein, about 170 Å thick. Internally the mitochondria contained membraneous structures embedded in a finely granular matrix.

I. Introduction

For several years it has been known that a number of enzymes, including those concerned in the later stages of respiration in plant cells, are associated with the mitochondria (Bonner and Millerd 1953). Recent work (Robertson *et al.* 1955) has demonstrated that mitochondria undergoing active oxygen uptake can maintain ions in concentrations different from those in the external medium. These observations, and others which show that mitochondria play an important part in cell metabolism, have increased interest in their structure in relation to their function. The recent development of successful thin-sectioning techniques allows the structure of small bodies such as mitochondria to be conveniently studied by electron microscopy. The particles can be separated from broken cells by differential centrifugation, so permitting the examination of their function.

The structure of plant mitochondria has not been widely investigated. Early work by Stafford (1951) and Anderson (1952) demonstrated that the particles were apparently surrounded by a membrane. Investigations of red beet (*Beta vulgaris* L.) mitochondria led Farrant, Robertson, and Wilkins (1953) to conclude that the membrane was about 270 Å in thickness. The external membrane is evident in electron micrographs of sectioned plant mitochondria published by Palade (1953), Sager and Palade (1954), and Mercer *et al.* (1955), all of whose pictures also show some evidence of internal structure. However, the structure of plant mitochondria is much more poorly documented than is that of their animal counterparts.

We record here further electron microscope observations on the morphology of mitochondria extracted from beet tissue under various conditions and compare these mitochondria with those in tissue sections.

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II. MATERIALS AND METHODS

(a) *Extracted Mitochondria*

Storage-root tissue of *B. vulgaris* was diced and disintegrated in a Waring Blendor with an equal volume of water or solution and squeezed through muslin to remove larger pieces of cell debris. The remaining large pieces of debris and nuclei were removed by centrifugation at 1600 *g* for 15 min. The supernatant was then centrifuged again at 1600 *g* for 20 min and the residue was resuspended in a small volume of the original solution. In the early experiments the oxygen uptake of this resuspended residue was checked in a Warburg apparatus but this was discontinued when it became clear that this method of preparation gave suspensions capable of oxygen uptake (Robertson *et al.* 1955). All these operations were carried out at 0–7 °C.

The blending was done in three different media—(1) water, (2) 0·45 per cent. potassium chloride (O.P. = 2·5 atm), or (3) 30 per cent. sucrose (O.P. = 26·8 atm)—and after the second centrifugation portion of the resuspended residue was examined under phase contrast. The remainder was kept at 0 °C until the specimens were prepared for electron microscopy.

Drops of the mitochondrial suspension were placed on specimen screens and fixed by adding an equal volume of either 1 per cent. formalin or 1–2 per cent. osmium tetroxide. Formalin fixation proved markedly inferior to osmium tetroxide fixation. After fixation the specimens were allowed to dry on the screen and the soluble materials were then removed by diffusion into water through the collodion membrane. The preparations were then shadowed with uranium and examined with the electron microscope.

For sectioning, the mitochondria were prepared as before but in 15 per cent. sucrose. After fixation for $\frac{1}{2}$, 1, or 2 hr in 1 per cent. osmium tetroxide solution containing 15 per cent. sucrose and buffered to pH 7·2 with acetate-veronal, the suspensions were transferred through series of aqueous solutions of sucrose and alcohol, in which the sucrose concentration was reduced as the alcohol concentration was increased through 50, 75, and 90 per cent. to absolute. The mitochondria were then embedded in butyl methacrylate polymer and sectioned using the method and microtome described by Hodge, Huxley, and Spiro (1954). The results obtained were independent of the fixation time employed.

(b) *Mitochondria in Tissue*

Mitochondria were also examined in tissue in thin sections of beet tissue. Fixation was carried out at room temperature in osmium tetroxide buffered to pH 7·2 with acetate-veronal. The basic formula used was:

Sodium acetate	0·028M
Sodium veronal	0·028M
Hydrochloric acid	0·022M
Osmium tetroxide	1 per cent.

The osmotic pressure was adjusted by adding sodium chloride to concentrations of (i) 0·105M or (ii) 0·20M, or by the addition of sucrose to give concentrations of (iii) 15 per cent. (iv) 30 per cent. The presence of sucrose is probably undesirable as it markedly reduced the rate of fixation by the osmium tetroxide. None of the above formulae was satisfactory; the results were too inconsistent for any one formula to be regarded as superior to the others. The addition of "Versene" to chelate the calcium liberated from the cut cells gave no improvement.

Slices of tissue 0·2–0·5 mm thick and 2 mm wide were cut from larger pieces of fresh beet while immersed in the fixative, fixed for periods from 4 to 24 hr and washed in solutions of the same composition as the fixative except for the absence of osmium tetroxide. Ethyl alcohol was added at hourly intervals in amounts sufficient to increase the alcohol concentrations in steps of 10 per cent. through to absolute. The specimens were then embedded at 45 °C in butyl methacrylate or in butyl methacrylate containing 10 per cent. of the methyl ester.

III. RESULTS

(*a*) *Size and Shape*

The appearance of the mitochondria in phase contrast is illustrated in Plate 1. When the particles were prepared in 30 per cent. sucrose, they appeared as small, refractile, almost homogeneous spheres but were not uniform in size. Those particles which were in reasonably sharp focus measured up to about 1 μ in diameter. The preparation in potassium chloride resulted in larger spheres, not uniform in density and ranging up to 2 μ in diameter. These particles closely resembled the animal mitochondria prepared in potassium chloride by Zollinger (1948). Preparations in water showed spheres that were larger and less dense.

It was noticed that both the sucrose and potassium chloride preparations, when kept under observation on the microscope slide at room temperature, gradually changed their appearance over about an hour. The number of larger diffuse spheres resembling those of the water preparations appeared to increase for a time. Subsequently the number of larger particles decreased, presumably due to disintegration.

The results are consistent with the experience with animal mitochondria that particles are maintained by isotonic or hypertonic solutions but that, even in the presence of such solutions, they become disorganized *in vitro*. No rods comparable with those shown by Harman (1950) with rat mitochondria were observed, though some of the plant particles in more dilute solutions resembled some of the stages in transformation shown by Harman.

The shadowed particles photographed in the electron microscope are shown in Plates 2 and 3. The appearance of the different preparations was consistent with that shown by phase contrast. The sucrose preparation (Plate 2, Fig. 1) showed the particles as compact bodies ranging in diameter from about 0·7 to 1·0 μ. The particles were not quite spherical. The shadow lengths were consistent with their "settling" or flattening on the bottom as they dried out on the screen. The near-spherical shape in the sucrose preparations was in distinct contrast to those in the more dilute solutions, where the particles, larger in diameter, appeared as flattened disks; the shadows were short. Apparently the larger spheres seen by phase contrast collapsed to disks on drying on the electron microscope screen.

The size and shape of the mitochondria prepared in sucrose are well illustrated in the sections from a sucrose preparation shown in Plates 4 and 5. These sections showed that most particles were isodiametric though some were ovoid with axial ratios up to 2.

A similar range of shape and size was exhibited by mitochondria seen *in situ* in tissue sections. This is evident from Plate 6 though these examples had lost their ground substance and were probably somewhat swollen. On occasions dumb-bell shaped examples were observed (e.g. Plate 6, Fig. 3) but this appearance could have resulted from the sectioning of a curved rod.

(*b*) *Internal Structure*

The phase contrast microscope did not reveal any internal structure in mitochondria freshly isolated in hypertonic sucrose (Plate 1, Fig. 1). However, when prepared in 0·45 per cent. potassium chloride or in water the mitochondria were no longer structureless but appeared as optically less dense bodies bounded by spherical shells of variable thickness as is illustrated at *A* in Plate 1, Figures 2 and 3. The collapsed membranes which resulted on drying the potassium chloride and water preparations (Plate 2, Figs. 2 and 3; Plate 3) were not empty but retained some of the internal material.

In addition to the mitochondria the suspensions contained many smaller particles (Plates 2 and 3). Though many of these probably represent fragments of other cytoplasmic components, the fact that the potassium chloride and water suspensions contained greater concentrations of them than occurred in the sucrose preparations suggests that some of them may have escaped from the mitochondria.

The interpretation of the observations made above was clarified by consideration of the micrographs of thin sections shown in Plates 4, 5, and 6. In the central areas of the mitochondria isolated in sucrose a finely granular or reticular matrix occurred while the peripheral areas also contained folds of membraneous material. In some cases (*A* in Plates 4 and 5) this inner membraneous material was not uniformly distributed around the circumference explaining the occurrence of non-uniform outer shells in the phase contrast micrographs (*A* in Plate 1, Figs. 2 and 3). As shown in Plate 6 many of the mitochondria in the tissue sections had lost much of their ground substance, presumably through rupture of their external membranes but the inner membraneous material was retained.

The fixatives used proved so poor for beet tissue that few intact mitochondria were observed in the tissue sections and no micrographs worthy of reproduction were obtained. The few pictures taken indicated that the interiors of intact mitochondria *in situ* were somewhat denser than those isolated in 15 per cent. sucrose (Plates 4 and 5), but, beyond showing that the internal membranes were distributed throughout the organelles and were not confined to the peripheral zones, little internal detail was revealed.

These observations suggest that the internal membranes are attached to the external membrane and are carried with it through the matrix when the mitochondria swell. In several places in the sections (e.g. at *X* in Plate 6, Figs. 2 and 3) the internal membranes appeared as pairs of dense lines 50-60 Å thick separated by a less dense band 80 Å or more wide but sets of extensive double membranes like those demonstrated in a variety of animal cells by Palade (1952, 1953) and by Sjöstrand (1953), Sjöstrand and Rhodin (1953), Sjöstrand and Hanzon (1954) were not seen.

(*c*) *The Surface Membrane*

The appearance of the isolated mitochondria in phase contrast was consistent with their possession of a surface membrane and this was confirmed by the electron micrographs of particles which had been isolated in 0·45 per cent. potassium chloride or in water. In some cases folds were visible in the collapsed membranes (Plate 2, Figs. 2 and 3; Plate 3). This evidence for a membrane and an estimate of its thickness as 270 Å was published by Farrant, Robertson, and Wilkins (1953).

The mitochondria sectioned *in situ* (Plate 6) clearly showed this outer membrane to be a double structure similar to that demonstrated in animal mitochondria by Sjöstrand (1953) and by Palade (1953). In our sections the outer membrane was not sufficiently well preserved to allow any reliable measurements of the thickness of the three components but in those places where the membrane was sectioned normally the dense layers were about 50 Å thick and were separated by a less heavily stained layer about 70 Å thick.

(*d*) *Other Organelles*

In addition to the mitochondria of the type described above, more complex bodies of the kind shown in Plates 7 and 8 were noticed. These were distributed amongst the mitochondria but were confined to the immediate vicinity of the nuclei. While it is possible that they were a type of mitochondrion the fact that they contained dense ovoid bodies (O in Plates 7 and 8) from 0·1 to 0·2 μ in diameter similar to those shown in chloroplasts by Finean, Sjöstrand, and Steinman (1953) and by Mercer *et al.* (1955) suggested they were some variety of plastid. They, too, were enveloped by a double membrane comprised of two 50 Å dense layers lying about 70 Å apart and the example shown in Plate 7 contained a similar internal membrane. As well as the ovoid bodies these organelles contained large numbers of dense angular granules of about 50 Å in diameter. There was also an inner region, apparently inaccessible to the ovoids and granules, occupied by tubes T shown in longitudinal section in Plate 8 and in cross section in Plate 7.

IV. DISCUSSION

The primary aim of this investigation was to determine how closely the structure of isolated mitochondria resembles that of mitochondria *in situ*, but the difficulties in preserving the organelles unaltered through the processes of fixation, dehydration, and embedding, make our interpretations subject to some uncertainty.

Palade (1953) found that the general morphological features of the mitochondria of the leaf tissue of two flowering plants closely resemble those encountered in a variety of animal cells and our observations show that beet mitochondria conform to the same pattern. (This also appears to be true of mitochondria from carrot root and onion root-tips which we also examined.) This is not surprising in view of the growing evidence of close parallels between the biochemistry of plant and animal respiration (Millerd and Bonner 1953; James 1954).

Reasons have been advanced by Sjöstrand (1953) for interpreting mitochondrial double membranes as consisting of a double layer of oriented lipid molecules stabilized by protein layers (the dense layers) on either side. Lipo-protein membranes are notoriously labile so this hypothesis may explain the difficulty of preserving plant mitochondria. The fixative penetrates the cell slowly and presumably alters the permeability of the tonoplast, exposing the incompletely fixed mitochondria to deleterious substances, e.g. acids, diffusing from the vacuole.

Rhodin (1954) demonstrated that the internal membranes of mouse kidney mitochondria were liable to disorganization during fixation unless certain conditions were fulfilled. Though similar precautions were taken, our beet mitochondria did not exhibit the pattern of internal parallel double membranes discovered by Palade (1952) in mammalian cells, the inner membranes actually observed may represent either septa or cristae (Palade 1953) which have altered during fixation and dehydration. Sjöstrand and Hanzon (1954) have objected to Palade's term cristae mitochondriales on the ground that they have found no evidence to support his claim that "the cristae are deep and rigid folds of the second internal mitochondrial membrane" (Palade 1953). While not as clear as may be desired our micrographs (Plate 6, Figs. 2 and 3) certainly support this claim of Palade. This point is of considerable interest particularly if plant mitochondria multiply by division.

When isolated in hypertonic sucrose by the techniques described above a considerable proportion of the mitochondria, though somewhat swollen, retained their matrix substance but derangement of the internal membranes seemed to occur. If this damage is due to the isolation procedure and not merely to inadequate fixation and if the mitochondrial enzymes are arranged in a definite spatial relationship (cf. Schneider and Hogeboom 1950) then the rates of at least some of the functions of such mitochondria would be affected.

Some have questioned the wisdom of identifying properties of extracted mitochondria with those of the same organelles in tissues and have used the deprecatory term "mush cytology". Our results demonstrate that much better methods of fractionation than those employed here are required if homogeneous preparations of intact plant mitochondria are to be obtained. Centrifugation in density gradients and other techniques such as electrophoresis may prove satisfactory. It appears that the electron microscope offers a suitable means of monitoring the preparative methods provided adequate fixation and dehydration can be evolved. When this has been done the ultimate goal of determining the location of the various mitochondrial enzymes will have been brought somewhat nearer. In this respect evidence has already been found suggesting that the hexokinase is located in the matrix (Saltman 1953) and that the succinoxidase is closely associated with the solid structures of the membranes, internal or external.

V. ACKNOWLEDGMENTS

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EXPLANATION OF PLATES 1-8

PLATE 1

Phase contrast micrographs of beet mitochondria. Particles marked *A* have non-uniform shells.

Fig. 1.—Isolated in 30 per cent. sucrose.

Fig. 2.—Isolated in 0·45 per cent. potassium chloride.

Fig. 3.—Isolated in water.

PLATE 2

Fixed beet mitochondria. Shadow lengths are four times the particle heights. Folds visible in the collapsed membranes shown in Figures 2 and 3. Electron micrograph.

Fig. 1.—Isolated in 30 per cent. sucrose.

Fig. 2.—Isolated in 0·45 per cent. potassium chloride.

Fig. 3.—Isolated in water.

PLATE 3

Fixed beet mitochondria and fragments of other cytoplasmic bodies isolated in 0·45 per cent. potassium chloride. Shadow ratio 4 : 1. Electron micrograph.

PLATES 4 AND 5

Sections of beet mitochondria isolated in 15 per cent. sucrose. Particles marked *A* would resemble those marked *A* in Plate 1, Figs. 2 and 3, in phase contrast. Electron micrographs.

PLATE 6

Figs. 1-3.—Sections of beet mitochondria *in situ* in beet-root. Fixed in osmium tetroxide solution containing 30 per cent. sucrose at pH 7·2. Internal double membranes shown at points marked *X*. Electron micrographs.

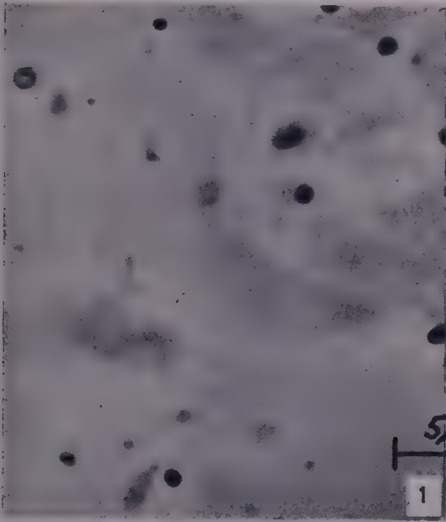
PLATE 7

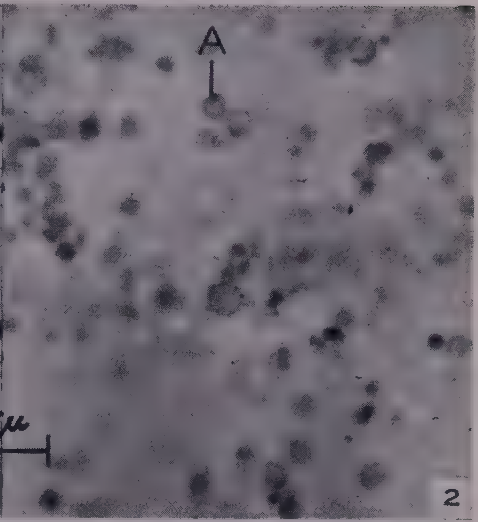
Cytoplasmic body, possibly a plastid, seen in section of beet tissue. Fixed in osmium tetroxide solution containing 30 per cent. sucrose at pH 7·2. Double membranes at *D*, granules at *G*, dense ovoid bodies at *O* and tubes in cross section at *T*. Electron micrograph.

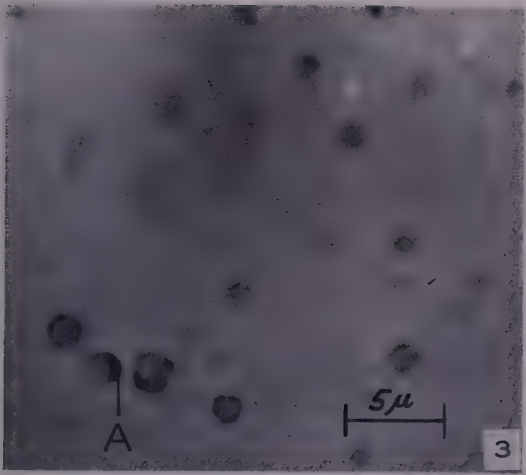
PLATE 8

Body similar to that of Plate 7, showing tubes *T* in longitudinal section. Mitochondrion in lower part of field. Electron micrograph.

MORPHOLOGY OF RED BEET MITOCHONDRIA







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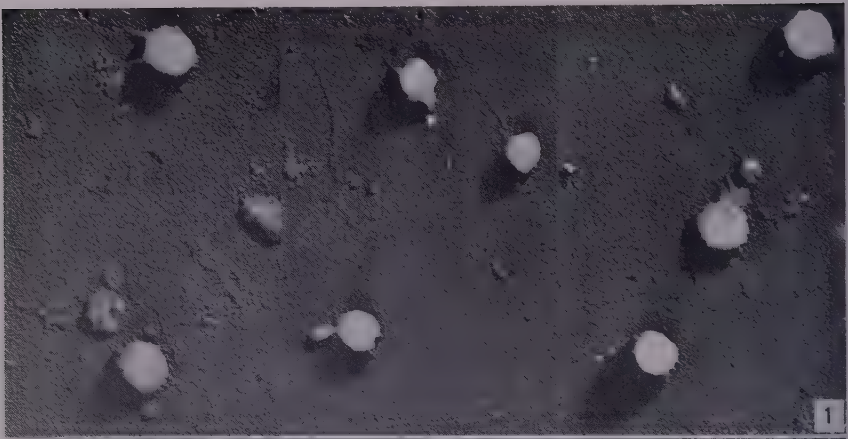

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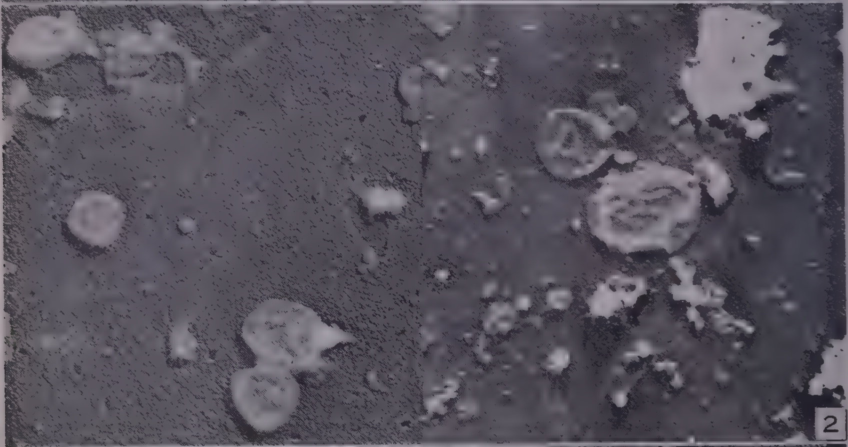

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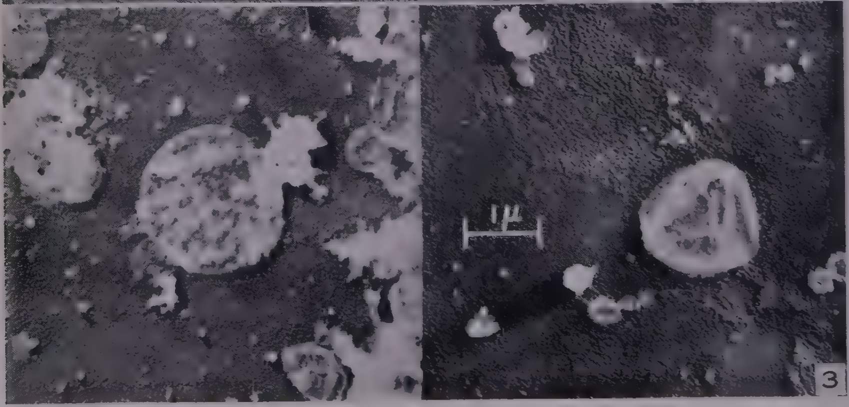

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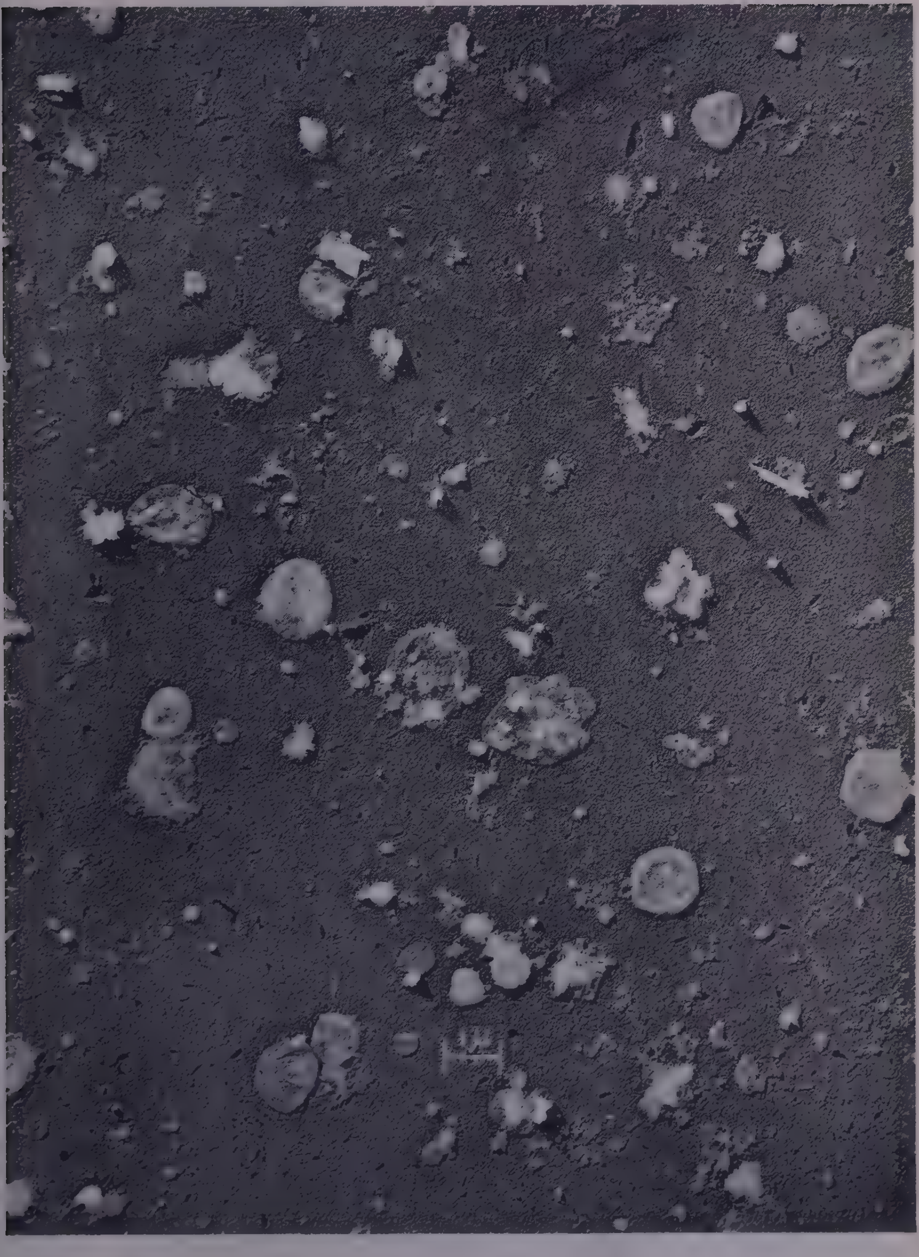

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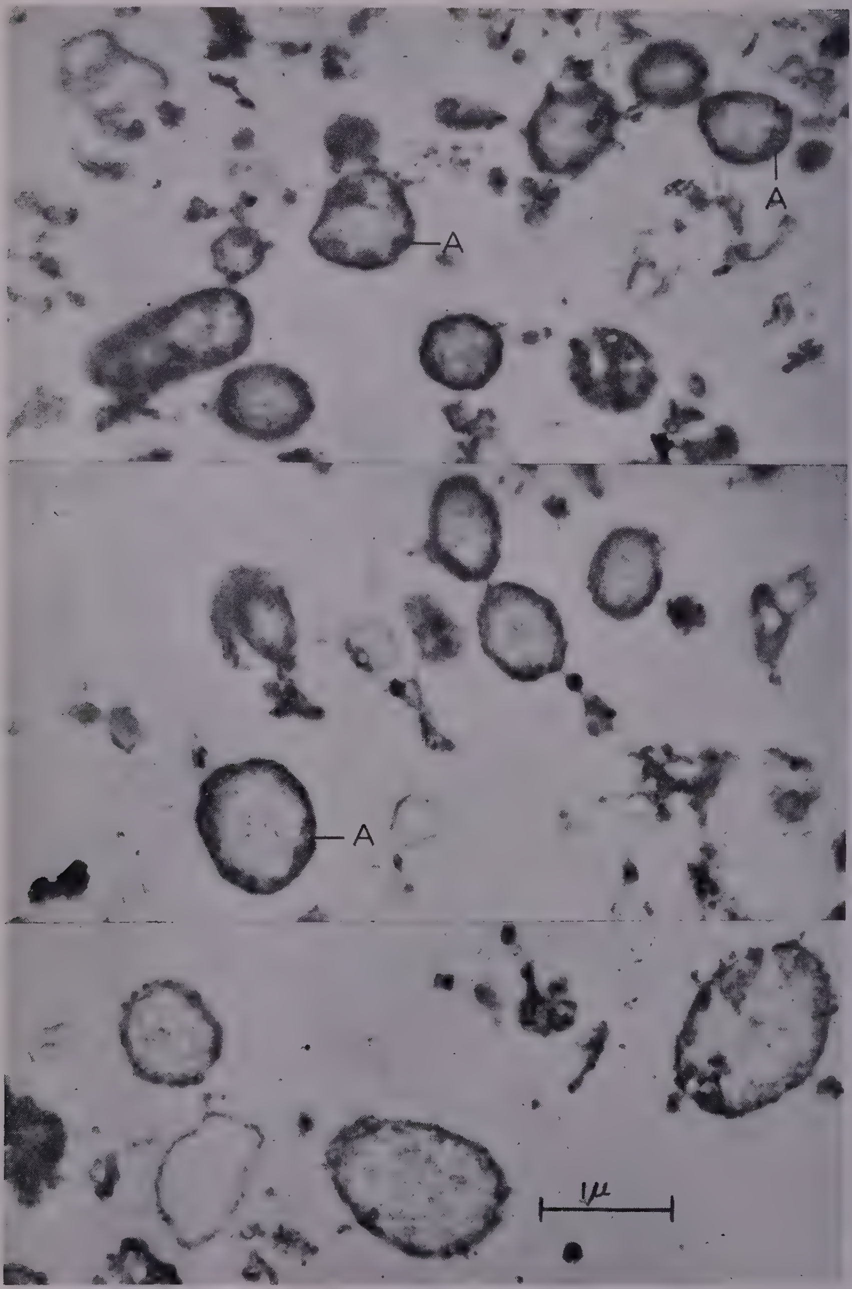

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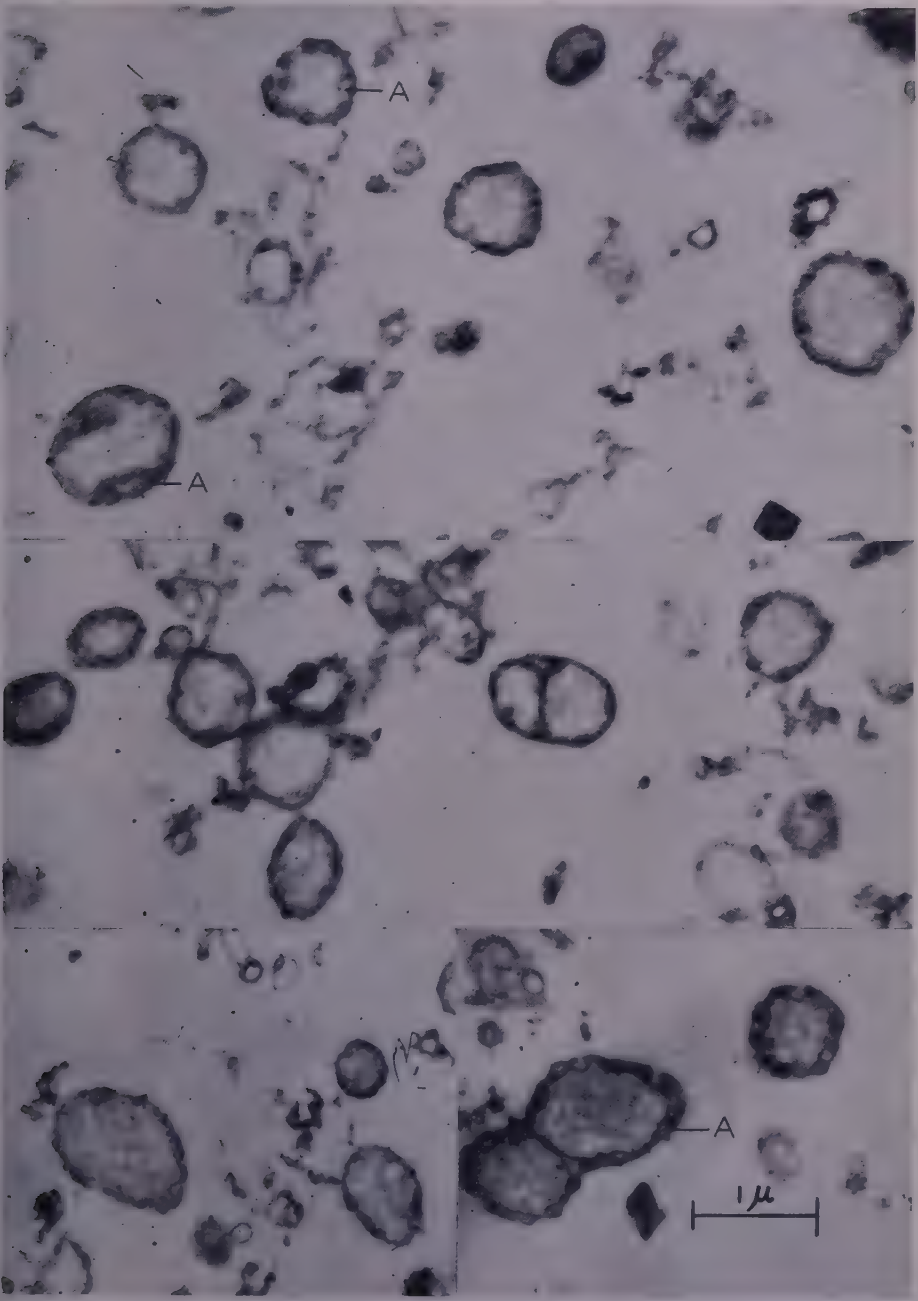

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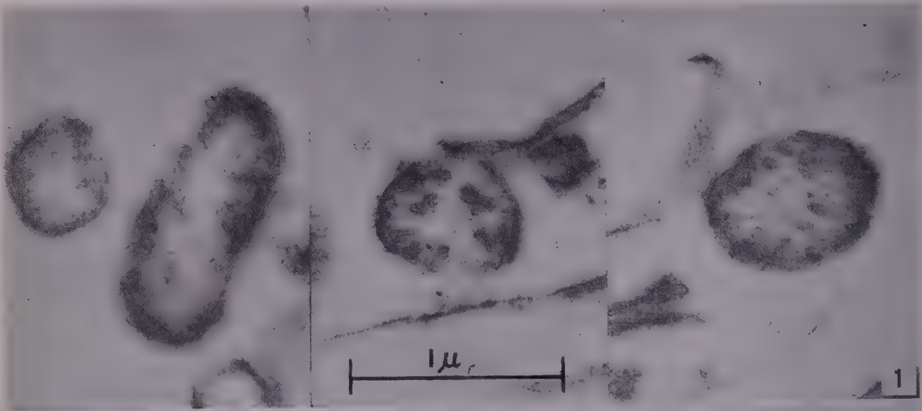

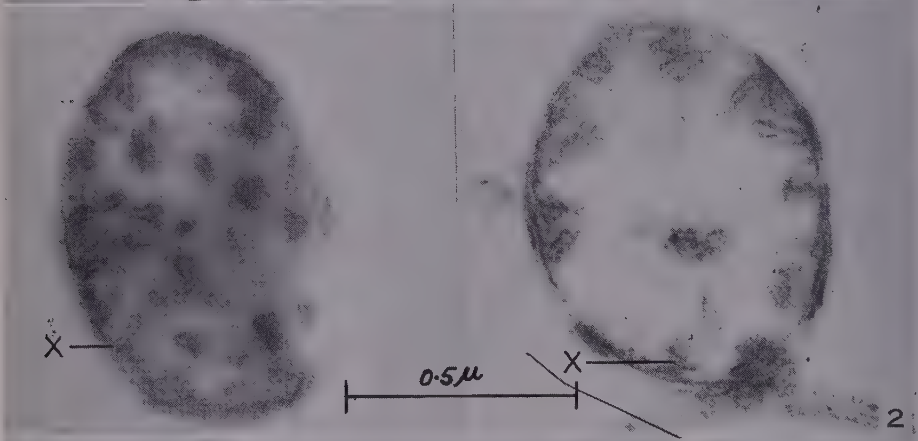

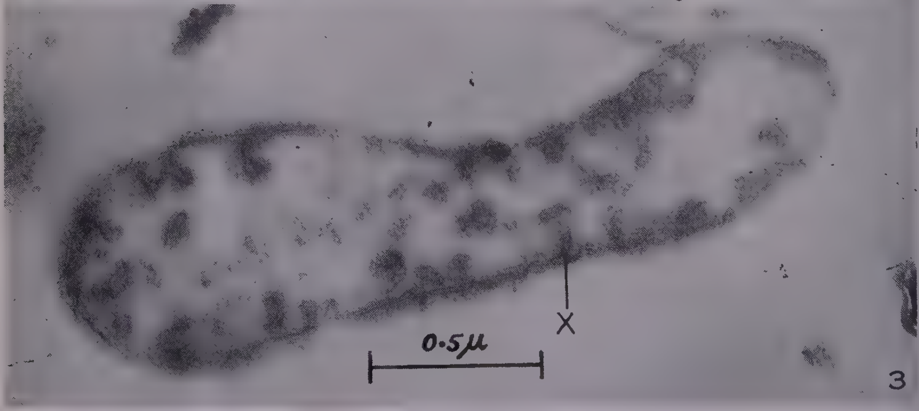

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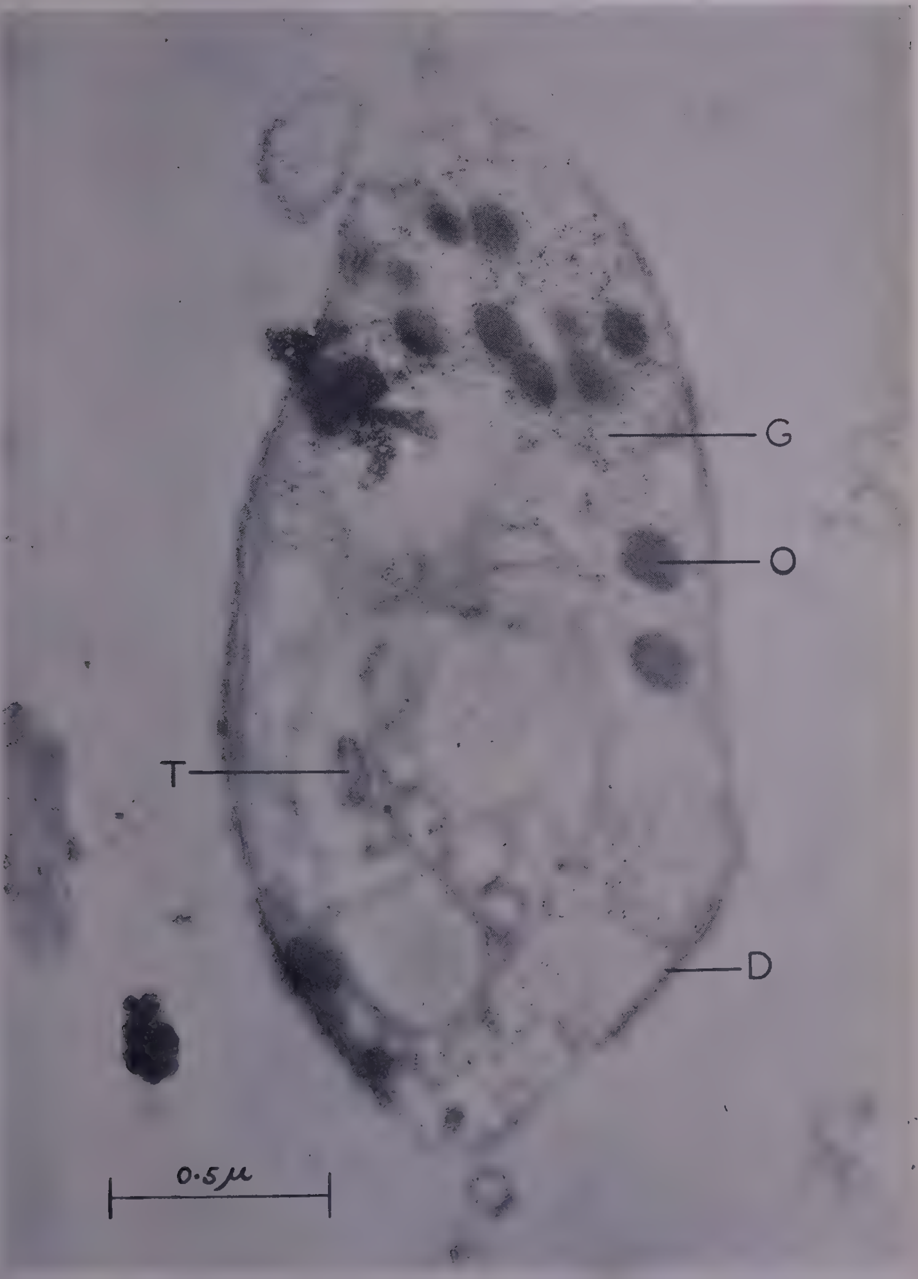

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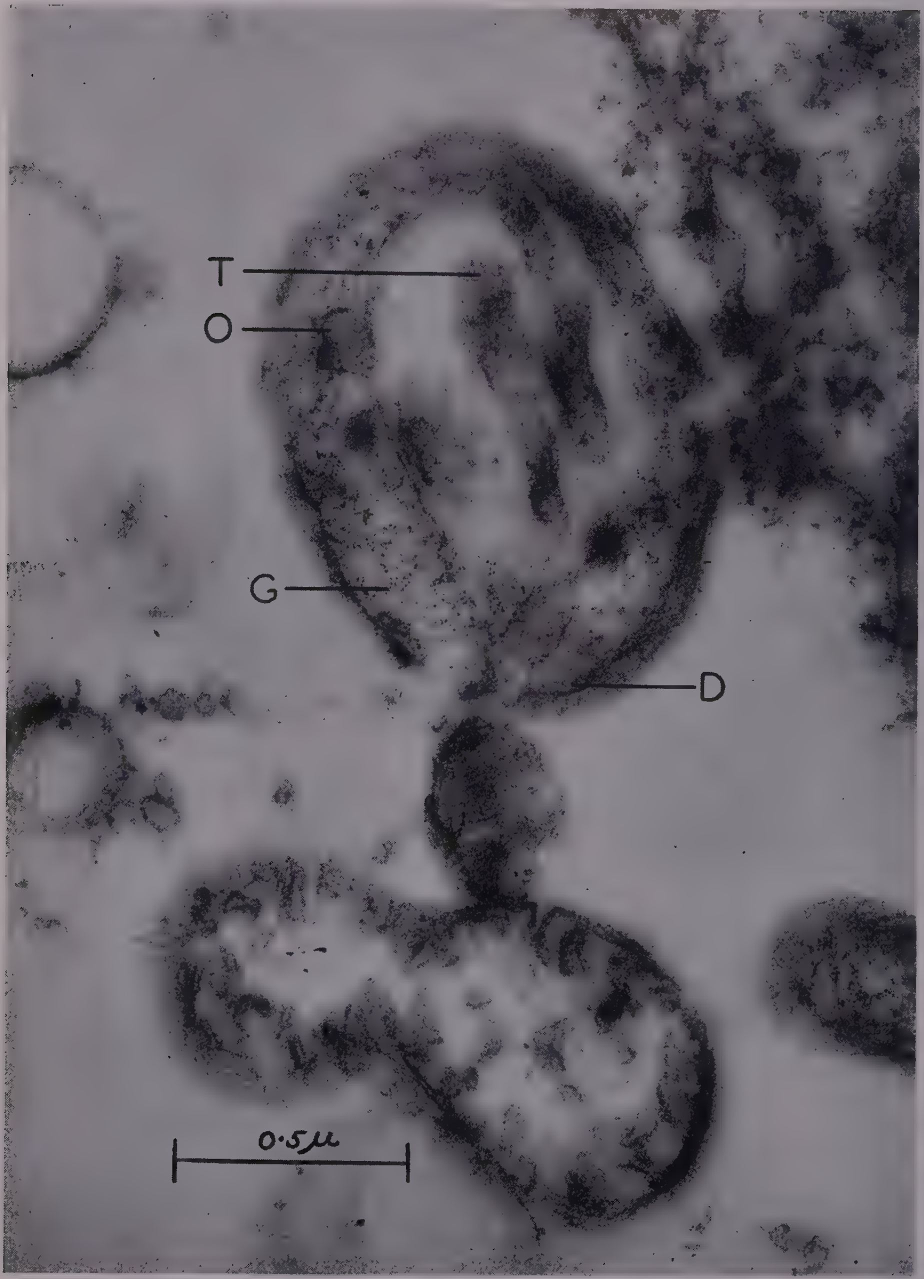

THE ANATOMY OF THE TIMBERS OF THE SOUTH-WEST PACIFIC AREA

IV. CUNONIACEAE, DAVIDSONIACEAE, and EUCRYPHIACEAE

By H. D. Ingle* and H. E. Dadswell*

[*Manuscript received December* 15, 1955]

Summary

The results reported cover 20 genera of the Cunoniaceae and the two monotypic families Davidsoniaceae and Eucryphiaceae, each closely related to the Cunoniaceae.

The anatomical features of the genera of these families have been summarized. In the Cunoniaceae these results have been compared with published information on the family and with features revealed by examination of the available species from other parts of the world.

A grouping of the genera of the Cunoniaceae based on their wood anatomy is given for diagnostic purposes and for comparison with botanical grouping. Anatomical relationships between the three families are discussed and points of similarity or difference between them and other families likely to be confused with them, are pointed out.

I. General

This paper is a further contribution to the series dealing with the wood anatomy of the timbers of the south-west Pacific area. Attention has been given in the past to the Australian genera belonging to the Cunoniaceae by Dadswell and Eckersley (1938) and Welch (1925) under the Saxifragaceae, which family is now generally accepted botanically as a purely herbaceous group distinct from the Cunoniaceae. The Cunoniaceae comprises some 24 to 26 genera, according to different taxonomists, and over 250 species; all genera are woody, including shrubs and small to sometimes large trees, with the exception of *Aphanopetalum* Endl., which is a vine.

The family is almost exclusively confined to the southern hemisphere, the main centre of distribution being in the region Australia, New Caledonia, and New Guinea (Fig. 1). Australia has five endemic genera but the number of species is low; New Caledonia has three out of seven genera endemic, *Codia* (11 species), *Cunonia* (16 species), and *Pancheria* (26 species), and a fourth genus, *Geissois*, with 10 out of 18 species endemic (Guillaumin 1948). The genus *Spiraeopsis* is centred mainly in New Guinea with 13 species, extending to the Philippines (10 species), with two species in the adjacent Celebes and Moluccas, and one in the Solomon Islands. Three genera, *Belangera* and *Caldcluvia* from South America and *Platylophus* from South Africa, do not occur in the south-west Pacific area. The genus *Cunonia* has an interesting distribution; it is practically confined to New Caledonia with 16 species, but has one species occurring in South Africa. *Weinmannia*, with close to 130 species, has by far the widest distribution; 78 species occur only in

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Central and South America, a further 16 in Madagascar and the Mascarene Islands, and the remainder in Malaysia and New Guinea, through Melanesia to New Zealand and the Cook Islands. There are no representatives of this genus in Australia or on the continents of Asia or Africa.

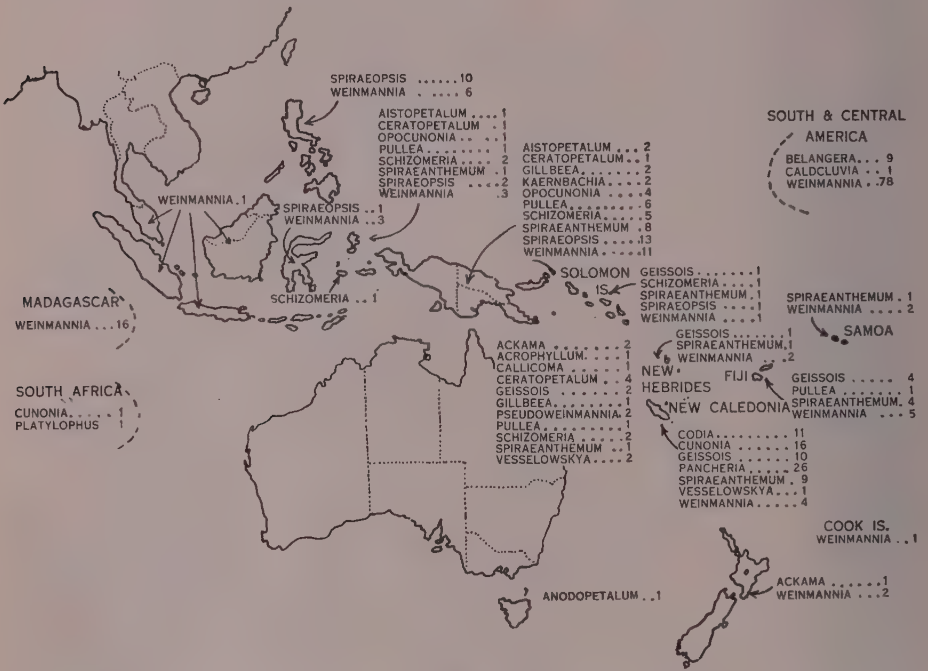

Fig. 1.—Distribution of genera and species of Cunoniaceae in the south-west Pacific.

The botanical classification of the family as put forward by Engler (1930) in his revision in "Die Natürlichen Pflanzenfamilien" has been used as a basis for comparison with affinities between the genera derived by examination of the secondary wood. This classification, in somewhat amended form, is set out in Table 1. The genera *Betchea* Schltr. and *Stollaea* Schltr. have been omitted since subsequent workers on this family, including Perry (1949) and Smith (1952), ascribe the New Guinea species of *Betchea* to *Spiraeopsis* Miq. and the genus *Stollaea* to *Opocunonia* Schltr.

Davidsonia F. Muell., a monotypic genus occurring in eastern Australia, which is excluded by Engler (and now placed by Bange (1952) in a separate family) has been included later in this study since its wood anatomy is so similar to that of some members of the Cunoniaceae. On this basis, the woody genera occurring in the area under consideration number 20, all of which are represented in this study, 68 species being examined.

From the timber standpoint none of the South American species are of any economic importance. *Cunonia capensis* L. red els, and *Platylophus trifoliatus*

TABLE 1

CLASSIFICATION OF THE CUNONIACEAE (AFTER ENGLER 1930)

		Genera Subsequently Recognized
A. Stamens ∞; petals wanting; carpels 2, superior, hypogynous; leaves digitate. Belangereae	*Belangera** Cambess *Geissois**† Labill.	
B. Stamens equal in number to or twice as many as sepals; carpels 5-3, also 2; superior, hypogynous. Spiraenthemeae		
a. leaves simple; fruit not winged	*Spiraeanthemum**† A. Gray	
b. leaves trifoliate; carpels 5, somewhat united; ovules always 2	*Aistopetalum**† Schltr.	
c. leaves trifoliate or digitate; fruit not winged; carpels 5-3, joined	(*Betchea* Schltr.)	= *Spiraeopsis* Perry & Smith
d. leaves pinnate	*Kaernbachia**† Schltr. *Gillbeea**† F. Muell.	
C. Stamens equal in number to or twice as many as sepals; carpels 2, superior; flowers simple or compound, but not in headed inflorescence. Cunonieae		
a. fruits bare or short-haired; sepals valved; stipules mostly separate (united in *Stollaea*); fruit a capsule or nut, stoned or fleshy	(*Stollaea* Schltr.)	= *Opocunonia* Perry & Smith
	*Ackama**† A. Cunn. *Spiraeopsis**† Miq. *Platylophus** D. Don *Caldcluvia* D. Don *Acrophyllum**† Benth. *Schizomeria**† D. Don *Ceratopetalum**† Smith *Anodopetalum**† A. Cunn. *Opocunonia**† Schltr.	
b. fruit a capsule, densely long-haired; sepals valved	*Pseudoweinmannia**† Engl.	
c. sepals imbricate; stipules indistinct, deciduous	*Vesselowskya**† Pamp. *Cunonia**† L. *Weinmannia**† L.	
D. Flowers in globular heads (small); stipules fused in pairs. Pancherieae	*Pancheria**† Brongn. & Gris *Callicoma**† Andr. *Codia**† Forst.	
E. Carpels 2, fused, semi-inferior, always with 3 distichous, upright ovules; petals wanting. Pulleae	*Pullea**† Schltr.	

* Genera examined at least in part in this work. † Genera occurring in the south-west Pacific.

(Thunb.) D. Don, white els, are of some commercial importance as timber in South Africa. Several genera in eastern Australia, e.g. *Ackama*, *Geissois*, *Ceratopetalum*, and *Schizomeria*, produce medium to large trees whose timbers are of cabinet class and are excellent for peeling as veneer and are useful for many specialty purposes such as rifle furniture, bobbins and shuttles, and other turned articles.

The family Davidsoniaceae has been recently created by Bange (1952) to accommodate the genus *Davidsonia* F. Muell., which was excluded by Engler from the Cunoniaceae in his revision of the family on the following grounds: "the stiff indumentum, the variable (alternate?) arrangement of the leaves, the short anther filaments, the lack of endosperm in the seeds all point against the relationship of the genus to the Cunoniaceae". To these Bange adds a further character of difference in the epitropous ovules, which in the Cunoniaceae are apparently apotropous (Bange). The wood anatomy of the genus closely resembles that of many genera of the Cunoniaceae.

The genus *Eucryphia* Cav. was formerly placed by Engler in the Hypericaceae; Planchon (1854) included it in the Cunoniaceae, which was then included under the Saxifragaceae. Since that time its affinities have been stated by various authors to lie with the Rosaceae (Bentham and Hooker 1862), and the Cunoniaceae (Focke 1893). Bausch (1938), in the most recent revision, states that this monotypic family is considered to be most nearly related taxonomically to the Cunoniaceae, and certainly the wood anatomy supports this view, hence its inclusion in this publication.

The Eucryphiaceae is now considered to consist of five species and one hybrid of the single genus *Eucryphia*. The monotypic genus *Paracryphia* Bak. f., found only in New Caledonia, was formerly also included; this has now been excluded by Bausch (1938); who suggests that it is better placed in the Winteraceae or Trochodendraceae.

Material for this investigation was obtained from the standard collection of the Division of Forest Products, C.S.I.R.O., which includes authenticated specimens received through the courtesy of forestry authorities in Malaya, North Borneo, Indonesia, the Philippines, New Guinea, British Solomon Islands, New Caledonia, and New Zealand.

II. THE ANATOMICAL CHARACTERISTICS OF THE GENERA EXAMINED

All available wood specimens of each species within a genus were examined macroscopically and microscopically and the results summarized, generic descriptions being prepared from these summaries. Details of the salient anatomical features of each genus have been set out in Table 2. Both in the generic descriptions and in the table averages of maximum vessel diameter, vessel member length, and fibre length have been included. In the case of the latter two series of measurements, macerated material was used; 10 vessel elements and 50 fibres were selected at random from each sample, and their lengths measured. The above samples were taken over several growth rings of mature wood. i.e. wood several inches from the centre where trees were of sufficient size. For the measurement of maximum tangential

TABLE 2

SUMMARY OF ANATOMICAL CHARACTERS OF 19 GENERA OF THE CUNONIACEAE OCCURRING IN THE SOUTH-WEST PACIFIC AREA

For comparison of features the genus *Davidsonia* has been included

Genus	No. of Species Examined	Vessels							Rays				Parenchyma				Fibres	
				Vessel Pits		Perforation Plates												
		Max. Tangential Diameter (μ)	% Solitary	Alternate or Transitional	Opposite to Scalariform	Exclusively Scalariform	Predominantly Simple	Mean Vessel Member Length (mm)	Width of Rays (No. of Cells)	Markedly Heterogeneous (3 + Cells)	Sheath Cells	Crystals	Paratracheal	Apotracheal Diffuse to Diffuse-in-Aggregate	Apotracheal Banded	Crystals	Pit Borders Distinct and on all Walls	Mean Length (mm)
Ackama	3	80–115	60–80	—	+	+	—	0·94–1·12	1, 3–4(6)	+	—*	—		+	—	±	±	1·53–1·73
Aistopetalum	1	127	50	+	—	—	+	0·88	1–3 (4)	+	—	—	—	+	—	+	—	1·50
Anodopetalum	1	70	65	—	+	±	∓	0·74	1–2 (3)	—	—	—	—	+	—	—	+	1·16
Callicoma	1	80	97	—	+	+	—	0·81	1, 3–4	+	—	—	—	+	—	—	+	1·35
Ceratopetalum	5	85–110	40–75	—	+	∓	+	0·84–1·05	1–3 (4)	—	—	±	—	+	+	+	∓	1·34–1·54
Codia	3	100–115	95	—	+	—	+	0·60–0·72	1–2 (3)	+	—	—	—	+		+	+	1·12–1·28
Cunonia	7	60–103	90	—	+	+	—	0·81–1·25	1–3 (4)	+	—	—	—	+	+	+	+	1·06–1·66
Geissois	8	80–190	15–35	+	—	—	+	0·81–1·05	1, 3–4(6)	+	—	—	—	+	—	+	—	1·05–1·76
Gilbeea	1	110	56	—	+	+	—	1·14	1, 3–4	+	—	—	—	+	—	—	—	1·62
Kaernbachia	1	127	95	—	+	+	—	1·80	1, 4-8(12)	+	+	—	+	—	—	—	+	2·85
Opocunonia	2	120–156	95	—	+	+	—	0·99–1·36	1, 3–4(6)	+	—	—	—	+	—	+	+	1·75–2·05
Pancheria	5	50–85	100	—	+	+	—	0·67–1·02	1–3	+	—	—	—	+	±	+	+	0·91–1·47
Pseudoweinmannia	2	85	20	+	—	—	+	0·62	1–3 (4)	±	—	—	—	+	—	+	—	1·42
Pullea	3	95–120	90–100		+	+	—	1·04–1·33	1, 3–6(8)	+	+	—	—	+	—	+	+	1·69–2·00
Schizomeria	6	115–155	15–64	+	—		+	0·73–1·12†	1–3	—	—	∓‡	—	—	+	+	—	1·24–1·92
Spiraeanthemum	2	75	95	—	+	+	—	1·10–1·32	1–3 (4)	+	—	—	∓	+	—	+	+	1·66–1·90
Spiraeopsis	8	100–150	27–60	+	—	—	±	0·70–1·02	1–3 (4)	±	—	∓§	—	+	—	+	—	1·07–1·80
Vesselowskya	2	95	95	—	+	+	—	1·05	1, 4–6	+	—	—	—	+	—	+	+	1·58
Weinmannia	7	50–130	95	—	+	+	—	0·70–1·29	1, 2–4(5)	+	—	—	—	+	—	+	+	1·10–1·81
Davidsonia	1	90	60	—	+	±	∓	0·81	1–3 (4)	—	—	—	—	+	—	+	+	1·66

* Present one sample *A. australiensis*. † Typically up to 1·01, 1·12 in one sample of *S. gorumensis*. ‡ Sparse, in three species. § Sparse, in one species

diameter of vessels 20 measurements were made from each sample and the 10 largest were averaged.

(a) *Ackama*

(i) *General.*—A genus of three species occurring in eastern Australia and New Zealand. The Australian species, *A. australiensis* C. T. White, rose alder, and *A. paniculata* Engl., brown alder, are moderately large trees of commercial importance for veneer, furniture, interior finish, and small turnery. The New Zealand species, *A. rosifolia* A. Cunn., is only a small to medium-sized second-storey tree and not of commercial importance. The timber of these species is red to pinkish brown sometimes with purplish tints; moderately light to moderately heavy, texture fine and uniform; grain somewhat interlocked; without figure, odour, or taste.

(ii) *Structure* (Plate 1, Fig. 3, and Plate 4, Fig. 6).—*Growth rings* indistinct. *Vessels* small and indistinct to the naked eye; maximum tangential diameter from 80 μ, (*A. rosifolia*) to 115 μ; mean member length 940-1120 μ; 60–80 per cent. solitary, and in radial multiples of 2–3, occasionally up to 5; very numerous (40+/sq. mm); vessel pitting opposite to generally scalariform; perforation plates oblique, predominantly scalariform with both fine and numerous and coarse and few bars, few transitional to simple. *Rays*, tending to two widths, uniseriate of square to upright cells, multiseriate 3–6 cells wide, heterogeneous, with uniseriate margins of square to upright cells; maximum height up to 30 cells; some tendency to sheath cells in one sample of *A. australiensis*; vessel-ray pits half-bordered, horizontally elongated, the border often distinct, opposite to scalariform in arrangement; extraneous material abundant throughout; crystals present, sparse in subdivided upright cells. *Parenchyma* apotracheal, diffuse to diffuse-in-aggregate in short discontinuous lines 1 cell wide; extraneous material present; crystals present, often abundant, in individual subdivided cells of strand; absent in *A. rosifolia*. *Fibres* moderately thin to moderately thick-walled, pits few to moderately numerous; small and indistinctly to distinctly bordered, mainly on radial walls; mean length 1·53–1·73 mm.

(iii) *Material.*—*A. australiensis* C. T. White (*A. quadrivalvis* White & Francis), four samples, eastern Australia; *A. paniculata* Engl. (*A. muelleri* Benth.), 14 samples, eastern Australia; *A. rosifolia* A. Cunn., one sample, New Zealand.

The species *A. australiensis* (*Weinmannia paniculosa* F. Muell.) was included by Engler in the former genus *Betchea*; this genus also included the four New Guinea species *B. fulva* Schltr., *B. rufa* Schltr., *B. papuana* (Pulle) Schltr., and *B. myriantha* Schltr. These four species are now regarded by Perry as belonging to the genus *Spiraeopsis*.

These two genera are close in their anatomical structure, *Ackama* only varying from *Spiraeopsis* in the predominance of scalariform perforation plates, the more obvious opposite to scalariform vessel pitting, and the higher percentage of solitary vessels. It would appear thus that the relegating of the genus *Betchea* in part to *Spiraeopsis* and in part to *Ackama* is justified on wood anatomical grounds, since the Australian species differ from those examined from New Guinea and eastern Malaysia in the above-mentioned characters.

(*b*) *Acrophyllum*

(i) *General.*—A monotypic genus occurring in eastern Australia; *A. venosum* is a small slender shrub growing in rocky localities at higher elevations.

(ii) *Structure.*—Examination of a small twig from herbarium material reveals a structure similar to the more primitive members of the family in having solitary vessels with opposite to scalariform pitting and scalariform perforation plates. *Parenchyma* sparse apotracheal, diffuse. *Fibres* with distinctly bordered pits on radial and tangential walls.

(iii) *Material.*—*A. venosum* Benth., one (H)* sample, eastern Australia.

(*c*) *Aistopetalum*

(i) *General.*—A small genus of two species of trees occurring in New Guinea and the Moluccas; two samples of *A. viticoides* Schltr. from the Moluccas were available for examination. The wood of these two samples is brown to red-brown; texture fine and uniform; grain somewhat interlocked; moderately light to moderately heavy; without figure or lustre.

(ii) *Structure.*—*Growth rings* indistinct. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 127 μ; mean member length 880 μ; 50 per cent. solitary, the remainder in radial multiples of 2-3 occasionally up to 4; numerous (30/sq. mm) and evenly distributed; vessel pitting alternate to sometimes opposite; perforation plates mainly simple to sometimes transitional to scalariform in smaller vessels. *Rays* 1–3-seriate, occasionally up to 4, uniseriates of square to upright cells, multiseriate with margins of square to upright cells; up to 30 cells high; vessel-ray pitting half-bordered but appearing simple, rounded to elongated, with some slight tendency to scalariform arrangement; pits to central cells of ray often distinctly bordered; extraneous material abundant; crystals not observed. *Parenchyma* apotracheal diffuse to sometimes diffuse-in-aggregate in fine short and discontinuous 1-celled lines; crystals present in individual subdivided cells of strand. *Fibres* thick-walled with moderately numerous pits on both radial and tangential walls though somewhat more numerous on the former; borders small and generally indistinct; mean length 1·50 mm.

(iii) *Material.*—*A. viticoides* Schltr., two samples, Moluccas.

(*d*) *Anodopetalum*

(i) *General* (Plate 1, Fig. 1, and Plate 4, Figs. 1 and 5).—A monotypic genus confined to Tasmania. *A. biglandulosum* A. Cunn., "horizontal", often has a curious habit of growth befitting its common name, when it forms dense and impenetrable interlacing scrub with stems lying horizontal and up to 5 in. in diameter; when erect the stems seldom exceed 12–14 in. in diameter. The wood is pale pinkish brown; moderately heavy; texture fine and even; grain straight to slightly interlocked; with slight figure on backsawn faces; without odour or taste; used locally for tool handles owing to its toughness.

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* (H) signifies twig material from herbarium specimens only.

(ii) *Structure.*—*Growth rings* well defined by narrow bands of denser late wood fibres and a concentration of parenchyma in this zone, and often by a ring of slightly larger pores in the early wood. *Vessels* invisible to the naked eye and indistinct even with lens; maximum tangential diameter 70 μ; mean member length 740 μ; 65 per cent. solitary, remainder in radial multiples of 2–3 with some tendency to tangential zoning; very numerous (50+/sq. mm); vessel pitting opposite to scalariform; perforation plates simple and scalariform with fine and moderately numerous bars; tyloses infrequent. *Rays* 1–2-seriate, occasionally up to 3; maximum height up to 25 cells; weakly heterogeneous with 2 or 3 rows of marginal cells of greater vertical dimensions than the central procumbent, to sometimes square or upright; vessel-ray pits half-bordered and opposite to scalariform in arrangement; crystals absent; extraneous material present, sometimes abundant. *Parenchyma* apotracheal diffuse, generally concentrated in outer part of growth ring and often forming short discontinuous lines or loose bands, and sparsely diffuse in early part of growth ring; crystals absent; extraneous material present. *Fibres* moderately thick-walled, with few small but distinctly bordered pits, chiefly on radial walls, but more prominent in the late wood where they tend to be equally numerous on radial and tangential walls; mean length 1·16 mm.

(iii) *Material.*—*A. biglandulosum* A. Cunn., 17 samples, Tasmania.

(*e*) *Callicoma*

(i) *General.*—A monotypic genus confined to eastern Australia. *C. serratifolia* (R.Br.) Andr. is a small to medium-sized tree and not of commercial importance. The timber is pinkish brown to sometimes rather orange-brown; light in weight; texture fine and uniform; grain interlocked; without odour or taste.

(ii) *Structure* (Plate 1, Fig. 2).—*Growth rings* usually indistinct, sometimes vaguely marked by more numerous pores in early part of the growth ring. *Vessels* very small and invisible to the naked eye, but distinct with lens; maximum tangential diameter 80 μ; mean member length 810 μ; predominantly solitary (97 per cent.) with few short multiples; extremely numerous (100+/sq. mm); vessel pitting infrequent, opposite to scalariform; perforation plates scalariform with fine bars 15–35 in number; tyloses present, not abundant; deposits of extraneous material sporadic. *Rays* of two widths, uniseriate of square and upright cells, multiseriate 3–4 cells wide, heterogeneous with uniseriate margins of 10 or more upright or square cells; maximum height up to 40 cells; vessel-ray pits half-bordered, the border often indistinct, apertures elongated horizontally and scalariform in arrangement; crystals absent; extraneous material abundant throughout. *Parenchyma* apotracheal, diffuse, tending to be concentrated in the outer portion of the growth ring, where some aggregation is evident; crystals absent; extraneous material present, variable in amount. *Fibres* moderately thick-walled, with numerous distinctly bordered pits on radial and tangential walls; mean length 1·35 mm.

(iii) *Material.*—*C. serratifolia* (R.Br.) Andr., three samples, eastern Australia.

(*f*) *Ceratopetalum*

(i) *General.*—A genus of five species, mainly confined to Australia (four species), with one species recorded from New Guinea and the Moluccas (Perry 1949). Three of the Australian species are medium-sized to moderately large trees, and their timbers are of considerable commercial importance. *C. apetalum* D. Don. is particularly favoured for furniture and cabinet work, and as veneer. The wood is pale to dark pinkish brown, usually weathering to a deeper shade; moderately light in weight; texture fine, with characteristic figure (particularly in *C. succirubrum*) on backsawn surfaces due to bands of parenchyma; grain somewhat interlocked; with characteristic sweet smell, described as similar to caramel, in *C. apetalum.*

(ii) *Structure* (Plate 2, Figs. 3 and 4, and Plate 4, Fig. 4).—*Growth rings* indistinct. *Vessels* small and invisible to just visible to the naked eye; maximum tangential diameter 83–113 μ; mean member length 840–1050 μ; 40–75 per cent. solitary in different samples, remainder in radial multiples up to 4 with a few clusters in *C. virchowii*; numerous to very numerous, varying from 30+/sq. mm in *C. succirubrum* to 80+/sq. mm in *C. apetalum*; vessel pitting opposite to scalariform; perforation plates predominantly simple but some scalariform present, chiefly in smaller vessels; tyloses present, variable; deposits of extraneous material sporadic in *C. virchowii*. *Rays* 1–3-seriate, occasionally up to 4; weakly heterogeneous with few marginal cells of greater vertical dimensions than central procumbent to occasionally squarish; maximum height from 20 cells in *C. virchowii* up to 40 cells in *C. apetalum*; vessel-ray pitting half-bordered and similar to vessel pitting, typically opposite to scalariform in arrangement; crystals sparse in *C. apetalum* and *C. virchowii*, chiefly in marginal cells; extraneous material generally abundant throughout. *Parenchyma* apotracheal, mainly in regularly to irregularly spaced bands 1–4 cells wide, chiefly 2–3; diffuse, sparse but regularly present; large crystals present, often in enlarged cells of strands; extraneous material present throughout and abundant in *C. succirubrum*. *Fibres* moderately thin to moderately thick-walled, pits few and indistinctly bordered in *C. virchowii* to moderately numerous and with small but distinct border in *C. apetalum*, predominantly in radial walls; mean length 1·34–1·54 mm.

(iii) *Material.*—*C. apetalum* D. Don., 27 samples, eastern Australia; *C. gummifera* Sm., one sample, eastern Australia; *C. succirubrum* C. T. White, 11 samples, north-east Australia; *C. tetrapterum* Matt., two samples, Moluccas; *C. virchowii* F. Muell., five samples, north-east Australia.

(*g*) *Codia*

(i) *General.*—A genus of 11 species of shrubs and small trees confined to New Caledonia; samples from four species were available for examination; none of these is of any commercial importance, but the wood is referred to as "chêne rouge" when cut. The wood of these is moderately dense; red to red-brown; texture fine; grain somewhat interlocked; without lustre or figure.

(ii) *Structure.—Growth rings* not evident. *Vessels* small and indistinct to the naked eye; maximum tangential diameter from 100–115 μ; mean member length 600–720 μ; 95 per cent. solitary; evenly distributed; 17–20/sq. mm; vessel pitting sparse; perforation plates predominantly to exclusively simple; tyloses generally abundant. *Rays* 1–2, occasionally up to 3-seriate, uniseriate generally of square to upright cells, multiseriate of procumbent with margins of several rows of square to upright cells; maximum height from 15–20 cells; 12–14 per mm; vessel-ray pits half-bordered, with large aperture, elongated, and scalariform in arrangement; crystals not observed; extraneous material abundant. *Parenchyma* abundant, apotracheal diffuse with some slight tendency to link up tangentially into short, uniseriate lines; crystal strands numerous. *Fibres* thick-walled, with numerous bordered pits on all walls; mean length 1·12–1·28 mm.

(iii) *Material.—C. discolor* (Brongn. & Gris.) ex Guillaum., one sample; *C. floribunda* Brongn. & Gris. (H), one sample; *C. incrassata* Pampan., two samples; *C. obcordata* Brongn. & Gris., two samples; *Codia* sp. aff. *C. ferruginea* Brongn. & Gris., one sample; all from New Caledonia.

(*h*) *Cunonia*

(i) *General.*—A genus of 17 species of small to medium-sized trees practically confined to New Caledonia, but with one species, *C. capensis* L., "red els", occurring in South Africa; this latter species is of some local commercial importance, the timber being used for furniture and turnery. The New Caledonian species are not of commercial importance, but one species, *C. austro-caledonica*, when cut, is referred to as "Chêne C.1". Material of seven of the New Caledonian species was available for examination. The wood of these species is dark-red to red-brown, moderately heavy; texture fine and uniform; grain straight to somewhat interlocked; without figure. When freshly cut, the wood of several of these species has a somewhat sweet smell, reminiscent of cow's breath. Another distinctive feature of some is an appearance macroscopically of having aggregate rays, the pores being segregated into radial zones of numerous and few pores alternating with radial zones of more and less numerous rays giving the appearance of broad or aggregated rays to the transverse section (see Plate 3, Fig. 1).

(ii) *Structure.—Growth rings* indistinct. *Vessels* very small and indistinct even with lens, to small and indistinct to the naked eye; maximum tangential diameter from 60-103 μ; mean member length 810–1250 μ; predominantly to almost exclusively solitary; very numerous (40+/sq. mm); vessel pitting seldom evident, when present usually opposite to scalariform; perforation plates scalariform with few to numerous bars (5–25); tyloses abundant. *Rays* 1–3-seriate, occasionally up to 4, uniseriate composed of square to upright cells; multiseriate with procumbent cells and with many rows of upright cells on margins; maximum height 37 cells; vessel-ray pits half-bordered, but appearing simple, with large aperture and narrow border, rounded, irregular to horizontally elongated; crystals not observed; extraneous material abundant in upright cells, sporadic in procumbent. *Parenchyma* moderately abundant, apotracheal, diffuse to diffuse-in-aggregate, with a tendency to link up into short tangential lines, also aggregations of parenchyma to form small tangential zones and bands of 2–6 cells wide, sometimes discontinuous; crystal strands numerous. *Fibres* thick-walled, with numerous, distinctly bordered pits on all walls; mean length 1·06–1·66 mm.

(iii) *Material.*—*C. austro-caledonica* Brongn. & Gris., two samples; *C. balansae* Brongn. & Gris., one sample; *C. macrophylla* Brongn. & Gris., one sample; *C. pulchella* Brongn. & Gris., one sample; *C. purpurea* Brongn. & Gris., one sample; *C. vieillardii* Brongn. & Gris., one sample; *Cunonia* sp. aff. *C. vieillardii* Brongn. & Gris., one sample; *Cunonia* spp. undet., three samples; all from New Caledonia.

Comparison of *C. capensis* L. with the above material reveals essentially the same structure wood anatomically, but does not show the aggregation or banding of apotracheal parenchyma characteristic of several of the New Caledonian species.

(*i*) *Geissois*

(i) *General.*—A genus of 18 species occurring from Fiji, Solomon Islands to New Caledonia (10 species), and Australia; the two Australian species, *G. benthami* and *G. biagiana* are medium-sized trees up to 100 ft. high and of some commercial importance as cabinet and furniture timbers and as veneer; also species of this genus come into Australia from time to time from New Caledonia, the timbers are very similar in appearance and properties to the Australian species. Wood generally light to dark pinkish brown, to pale yellowish white or straw near the bark; moderately light to moderately heavy; texture fine and uniform; grain somewhat interlocked; without odour, lustre, or figure.

(ii) *Structure* (Plate 2, Fig. 2).—*Growth rings* generally indistinct. *Vessels* small to intermediate in size indistinct to visible to the naked eye; maximum tangential diameters from 70 μ in *G. benthami* to 190 μ in *G. hirsuta*; mean member length 640–1050 μ; 13–33 per cent. solitary, remainder in radial multiples up to 4, occasionally up to 5, with a few clusters in all species; moderately numerous to numerous (6–21/sq. mm); vessel pitting typically alternate with some slight opposite tendency; perforation plates typically simple with few transitional to scalariform plates in smaller vessels in all species; tyloses absent. *Rays* of two distinct widths, uniseriate numerous and composed of square and upright cells; multiseriate mostly 3–4, sometimes up to 6 cells wide, heterogeneous with uniseriate margins of square and upright cells; maximum height varying from 15–50 cells; vessel-ray pits half-bordered with large apertures, apparently simple, rounded to elongated and sometimes in scalariform arrangement; crystals absent; extraneous material abundant. *Parenchyma* apotracheal, diffuse or diffuse-in-aggregate mainly in short discontinuous, tangential lines; crystal strands abundant; extraneous material present. *Fibres* moderately thick-walled with few indistinctly bordered pits, mainly on radial walls; mean length 1·05–1·76 mm.

(iii) *Material.*—*G. balansae* Brongn. & Gris., one sample, New Caledonia; *G. benthami* F. Muell., 13 samples, eastern Australia; *G. biagiana* F. Muell., four samples, eastern Australia; *G. hirsuta* Brongn. & Gris., one sample New Caledonia; *G. pentaphylla* C. T. White, one sample, Solomon Islands; *Geissois* spp. unassigned, three samples, New Caledonia.

(*j*) *Gillbeea*

(i) *General.*—A genus of three species of small to moderately large trees. *G. adenopetala* from northern Queensland is only a small tree, the two New Guinea species are reputed to be up to 90 ft high; the wood of the former species is pale brown in colour; texture fine and uniform; grain moderately straight; without figure or lustre; moderately light.

(ii) *Structure.*—*Growth rings* indistinct. *Vessels* small and invisible to the naked eye; maximum tangential diameter 110 μ; member length 1140 μ; 56 per cent. solitary, remainder in radial multiples up to 3, and occasionally up to 5; evenly distributed; very numerous (50+/sq. mm); vessel pitting scalariform; perforation plates scalariform with few (up to 12) moderately fine, but relatively widely spaced, bars; tyloses absent. *Rays* tending to two distinct widths, uniseriate of upright cells, and multiseriate 3–4 cells wide with uniseriate margins of square to upright cells; maximum height up to 30 cells; vessel-ray pitting half-bordered and in scalariform arrangement; crystals absent; deposits of extraneous material abundant. *Parenchyma* apotracheal diffuse with some tendency to diffuse-in-aggregate in fine short uniseriate lines between rays; crystals absent; deposits of extraneous material abundant. *Fibres* thin-walled with few small indistinctly bordered pits, mainly on radial walls; mean length 1·62 mm.

(iii) *Material.*—*G. adenopetala* F. Muell., two samples, north-eastern Australia.

(*k*) *Kaernbachia*

(i) *General.*—A genus of two species of small to medium-sized trees, confined to New Guinea; material of one species was available for examination. The wood of this species is light in weight and straw-coloured to pale brown; texture moderately fine and uniform; rays showing fairly prominently on radial surfaces.

(ii) *Structure* (Plate 2, Fig. 5, Plate 3, Figs. 2 and 4, Plate 4, Fig. 3).—*Growth rings* not evident. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 127 μ; mean member length 1800 μ; 95 per cent. solitary, with many apparent tangential multiples due to overlapping ends of members; oval, radially elongated to somewhat angular in cross section; moderately numerous to numerous (15–28/sq. mm); vessel pitting in overlapping ends scalariform; perforation plates exclusively scalariform with numerous, fine bars up to 35 or more in number; tyloses not observed. *Rays* of two distinct widths; uniseriate numerous, composed entirely of upright cells; multiseriate, few, 4–10 cells wide, occasionally up to 12, composed of procumbent cells with three to several rows of upright cells at margins; sheath cells consistently present in all multiseriate rays, vessel-ray pits half-bordered, with wide aperture and indistinct border, horizontally elongated, opposite to scalariform in arrangement; deposits of extraneous material scanty; crystals not observed. *Parenchyma* almost exclusively paratracheal with few diffuse strands; crystals absent; deposits of extraneous material scanty. *Fibres* moderately thin to moderately thick-walled, non-septate with distinctly bordered pits on all walls; mean length 2·85 mm.

(iii) *Material.*—*Kaernbachia pentandra* Schltr., three samples, New Guinea.

(*l*) *Opocunonia*

(i) *General.*—A small genus of trees occurring in New Guinea and the Moluccas; samples from two species were available for examination; the wood of these species is pale red to red-brown; texture moderately fine and uniform; moderately light; without lustre or figure.

(ii) *Structure.*—*Growth rings* absent. *Vessels* small and indistinct to just visible to the naked eye; maximum tangential diameter 120–160 μ; mean member length 960–1360 μ; 90–95 per cent. solitary; numerous (20–27/sq. mm); vessel pitting sparse, generally opposite when present; perforation plates exclusively scalariform with few bars (5–12 in number); tyloses not observed. *Rays* 1–5-seriate, occasionally up to 6, with some tendency for segregation into two distinct widths; uniseriate of upright cells; multiseriate of procumbent cells with uniseriate margins of square to upright cells from 3 to several in number; vessel-ray pits half-bordered but appearing simple with wide aperture and narrow border horizontally elongated to scalariform; crystals not observed; deposits of extraneous material abundant. *Parenchyma* apotracheal, abundant, usually distinctly diffuse-in-aggregate, with numerous short and discontinuous lines 1 cell wide, some diffuse; crystal strands numerous sometimes chambered in individual cells of strand. *Fibres* moderately thick-walled with numerous distinctly bordered pits on radial and tangential walls; mean length 1·75–2·05 mm.

(iii) *Material.*—*O. kuniensis* Schltr., three samples New Guinea and Moluccas; *Opocunonia* sp. aff. *O. papuana* Kan. & Hat., one sample New Guinea; *Opocunonia* sp. aff. *O. kaniensis* Schltr., one sample New Guinea.

(*m*) *Pancheria*

(i) *General.*—A genus of 26 species of shrubs or small trees confined to New Caledonia; timber from the few species of commercial size, when cut, is referred to as "Faux teck", and is occasionally seen on the Australian market. The wood of the five species available for examination is dark brown to dark red-brown; moderately dense to dense; texture fine and uniform; grain straight to somewhat wavy and interlocked; without odour, figure, or lustre.

(ii) *Structure.*—*Growth rings* indistinct. *Vessels* invisible to indistinct to the naked eye; maximum tangential diameter 50–85 μ; mean member length 670–1020 μ; exclusively solitary; numerous (30–60+/sq. mm); vessel pitting sparse, opposite to scalariform in overlapping ends of vessel members; perforation plates scalariform with moderately numerous bars (less than 15 in number). *Rays*, 1–3-seriate, heterogeneous with few to several rows of square and upright cells at margins, uniseriate all of square and upright cells; vessel-ray pitting half-bordered with large aperture and narrow border horizontally elongated to scalariform in arrangement; crystals not observed; extraneous material abundant. *Parenchyma* apotracheal, mainly diffuse but tending to aggregate into loose tangential bands, often discontinuous; crystal strands abundant. *Fibres* thick-walled with numerous distinctly bordered pits on radial and tangential walls; mean length 0·91–1·47 mm.

(iii) *Material.*—*P. engleriana* Schltr., one sample; *P. insignis* Schltr., one sample; *P. seberti* Guillaum., one sample; *P. ternata* Brongn. & Gris., one sample; *Pancheria* spp. unassigned, five samples; all from New Caledonia.

(*n*) *Pseudoweinmannia*

(i) *General.*—A genus of two species of trees confined to eastern Australia. *P. lachnocarpa* Engl., mararie, (formerly *Geissois lachnocarpa* J. H. Maiden) is often quite large, attaining a total height of 100–120 ft. *P. apetala* Engl. is only a small tree and not of commercial importance. The wood of mararie is dark red to red-brown, sometimes with a purplish tinge; moderately dense to dense, with a fine and uniform texture; grain somewhat interlocked; without figure, lustre, or taste. The timber is excellent for vehicle framing, turnery and carving, and for printers' blocks.

(ii) *Structure* (Plate 2, Fig. 6).—*Growth rings* indistinct or sometimes marked by bands of denser fibres lacking diffuse to reticulate parenchyma. *Vessels* small and indistinct to the naked eye, maximum tangential diameter 85 μ; mean member length 620 μ; evenly distributed; solitary (20 per cent.) and in radial multiples often 3–4 but occasionally up to 6 or 8; numerous (30–40/sq. mm); perforation plates simple; vessel pitting alternate. *Rays* 1–4-seriate, uniseriate of square to upright cells only, but not sharply differentiated from the multiseriate rays with margins of 1 to several rows of square to upright cells; maximum height up to 30 cells; vessel-ray pits with large aperture and narrow border, rounded to irregular, mainly confined to square and upright cells; deposits of extraneous material abundant; crystals not observed. *Parenchyma* apotracheal generally diffuse-in-aggregate or in fine discontinuous uniseriate lines, generally absent or infrequent in the last part of the growth ring; crystal strands numerous. *Fibres* thick-walled non-septate, with moderately numerous pits on radial and tangential walls though more numerous on the radial; borders indistinct; mean length 1·42 mm.

(iii) *Material.*—*P. apetala* Engl. one (H) sample, eastern Australia; *P. lachnocarpa* Engl., nine samples, eastern Australia.

(*o*) *Pullea*

(i) *General.*—A genus of eight or nine species of small to medium-sized trees occurring in the Moluccas, New Guinea, north-east Australia, and Fiji. Samples from three species were available for examination. The wood of these species is red to red-brown; texture fine and uniform, moderately dense; grain generally straight; without figure, lustre or taste. *P. stutzeri* is of some commercial importance in Australia for general interior work.

(ii) *Structure* (Plate 1, Fig. 6).—*Growth rings* indistinct or not evident. *Vessels* small and indistinct to just visible to the naked eye; maximum tangential diameter 95–120 μ; mean member length 1040–1330 μ; almost entirely solitary; evenly distributed; numerous (30–60/sq. mm); vessel pitting sparse, where present opposite to scalariform; perforation plates exclusively scalariform with few coarse bars, to moderately numerous with fine bars in *P. glabra*. *Rays* markedly of two distinct widths, uniseriate of upright cells, numerous; multiseriate of 3–6 cells wide, occasionally up to 8 in *P. stutzeri*, with tall uniseriate margins of upright cells;

sheath cells present in a few samples of *P. stutzeri*; vessel-ray pits half-bordered with narrow border and large rounded to horizontally elongated apertures often scalariform in arrangement; crystals not observed; extraneous material abundant. *Parenchyma* moderately abundant and apotracheal, diffuse, but tending to diffuse-in-aggregate in fine short discontinuous lines, 1 cell wide in some samples; crystal strands common. *Fibres* moderately thick-walled, non-septate, with numerous distinctly bordered pits on radial and tangential walls; mean length 1·69–2·00 mm.

(iii) *Material.*—*P. glabra* Schltr., one sample, New Guinea; *P. stutzeri* (F. Muell.) L. S. Gibbs., five samples, north-eastern Australia; *P. versteeghii* Perry, one sample, Moluccas.

(*p*) *Schizomeria*

(i) *General.*—A genus of some 15 species of medium-sized to large trees occurring chiefly in New Guinea and Australia but extending to Ambon Island and the Solomon Islands. The two Australian species, *S. ovata* D. Don. and *S. whitei* Mattfeld, are both large trees and of considerable importance for furniture manufacture, interior work, and veneer. The wood of the species available for examination is straw-coloured to pale brown or often pinkish brown, developing a greyish black heart of very irregular shape in *S. ovata*, apparently pathological in nature; texture moderately fine; grain straight to somewhat interlocked; moderately light; slight figure on backsawn faces; sapwood of *S. ovata* very susceptible to *Lyctus* attack; without odour or taste.

(ii) *Structure* (Plate 2, Fig. 1, Plate 3, Fig. 3, Plate 4, Fig. 2).—*Growth rings* generally indistinct to sometimes marked by denser bands of fibres in *S. floribunda*. *Vessels* small and indistinct to just visible to the naked eye; maximum tangential diameter 115–155 μ; mean member length 730–1010 μ (1120 μ in one sample of *S. guromensis*); solitary and in radial multiples of 4–6 occasionally up to 8; solitary varying from 15–64 per cent. in different species and samples; numerous (20–35/sq. mm); vessel pitting typically alternate with sometimes an opposite tendency; never scalariform; perforation plates predominantly simple, some scalariform and transitional; tyloses occasionally present in *Schizomeria* sp. aff. *serrata*. *Rays* 1–3 seriate, sometimes only up to 2-seriate, uniseriate similar to multiseriate; weakly heterogeneous with few rows of squarish cells at margins of rays; maximum height up to 25 cells; vessel-ray pits similar to intervessel sometimes with narrow border and large aperture, round to elongated or irregular in shape, seldom scalariform in arrangement; crystals sparse in three species; extraneous material sporadic. *Parenchyma* apotracheal, generally in continuous to sometimes discontinuous wavy bands 1–4 cells wide, regularly to irregularly spaced; crystals abundant in most species in individual subdivided cells of strand; extraneous material present. *Fibres* moderately thin-walled, non-septate with few pits mainly on radial walls, indistinctly bordered to occasionally distinct with small border; mean length 1·24–1·66 mm (1·92 mm in one sample of *S. guromensis*).

(iii) *Material.*—*S. floribunda* Schltr., three samples, New Guinea; *S. guromensis* Schltr., two samples, Moluccas; *S. ovata* D. Don., 20+ samples, eastern Australia; *S. pulleana* O. C. Schmidt, (= *S. brassii* Mattfeld), one sample, Solomon Islands; *S. serrata* Hochr., two samples, Ambon; *Schizomeria* sp. nov., aff *S. serrata* Hochr., two samples, New Guinea; *S. whitei* Mattfeld, two samples, north-eastern Australia; *Schizomeria* spp. unassigned, three samples, New Guinea and Solomon Islands.

(*q*) *Spiraeanthemum*

(i) *General.*—A genus of 27 species centred mainly in New Guinea (eight species) and New Caledonia (nine species), extending to Fiji, Samoa, and eastern Australia. None are of any commercial importance as timber. Samples from two species were available for examination. The wood of these is pale pinkish brown; texture fine and uniform; moderately heavy; without figure, lustre, or taste.

(ii) *Structure.*—*Growth rings* indistinct. *Vessels* very small, invisible to the naked eye; maximum tangential diameter 75 μ; mean member length 1100-1320 μ; evenly distributed; somewhat angular in cross section; 95 per cent. solitary; pitting scalariform when present; perforation plates exclusively scalariform with numerous fine bars. *Rays* 1–3-seriate, occasionally up to 4; uniseriate of square to upright cells; multiseriate heterogeneous with numerous rows of square to upright cells; vessel-ray pitting half-bordered with narrow border and wide aperture, horizontally elongated and often in scalariform arrangement; extraneous material abundant; crystals not observed. *Parenchyma* apotracheal diffuse, sometimes in contact with vessels, but not paratracheal; crystal strands present. *Fibres* thick-walled, non-septate, with small, but distinctly bordered pits on radial and tangential walls; mean length 1·66–1·90 mm.

(iii) *Material.*—*S. idenburgense* Perry, one sample, Moluccas; *S. pulleanum* Schltr., one sample, New Guinea.

(*r*) *Spiraeopsis*

(i) *General.*—A genus of 23 species, of small to medium-sized trees, occurring mainly in New Guinea and the Philippines. Samples from eight species were available for examination. The wood of these species is moderately light and soft, pinkish brown to pale red-brown in colour; texture fine and uniform; grain slightly interlocked; no figure, lustre, or taste.

(ii) *Structure* (Plate 1, Fig. 4).—*Growth rings* indistinct, occasionally marked by some radial flattening of the last few rows of fibres. *Vessels* small and indistinct to just visible to the naked eye; maximum tangential diameter from 100–148 μ; mean member length from 700–1020 μ; evenly distributed; solitary (27–60 per cent.) and in radial multiples up to 4, with occasional small clusters; perforation plates predominantly simple, with plates transitional to scalariform in some species; vessel pitting chiefly alternate or loosely arranged to sometimes mainly opposite, or occasionally scalariform, often in the one sample. *Rays* 1–4-seriate, mainly 1–3; uniseriate moderately numerous, varying from all short procumbent or squarish cells to all upright in different species; multiseriate of procumbent cells with uniseriate margins of few to many square and occasionally upright cells; pits between ray cells numerous and conspicuous; vessel-ray pits half-bordered with large rounded to elongated apertures, and narrow borders, occasionally in scalariform arrangement; extraneous material moderately abundant; crystals only observed in one sample of *S. glabrescens*. *Parenchyma* moderately abundant; apotracheal diffuse to occasionally diffuse-in-aggregate in fine short discontinuous lines, one cell wide; crystals present, in subdivided cells of strands. *Fibres* thin-walled, non-septate, with simple to indistinctly bordered pits, chiefly on radial walls; mean length 1·07–1·80 mm.

(iii) *Material.*—*S. aglaeiformis* (Kan. & Hat.) Perry, one sample, Moluccas; three samples, New Guinea: *S. brassi* Perry, one sample, New Guinea; *S. celebica* Miq., one sample, Bougainville; *S. glabrescens* Perry, three samples, New Guinea; *S. myriantha* (Schltr.), Perry, one sample, Moluccas; *S. papuana* (Pulle) Perry, one sample, New Guinea; *S. pubescens* Perry, two samples, New Guinea; *S. rufa* Schltr.) Perry, one sample, New Guinea.

(*s*) *Vesselowskya*

(i) *General.*—A genus of three species, only two of which were available for examination. *V. rubifolia* (F. Muell.) Pamp. (formerly ascribed to *Geissois*) is a small tree occurring in New South Wales, *V. serratifolia* Guill., a medium-sized tree occurring in New Caledonia. The wood of the latter is pinkish brown to dark brown; moderately light: texture fine and uniform; grain interlocked; without figure, odour, or taste.

(ii) *Structure.*—*Growth rings* indistinct. *Vessels* small and indistinct to the naked eye; maximum tangential diameter 95 μ; mean member length 1050 μ; evenly distributed; entirely solitary; numerous (40+/sq. mm); vessel pitting opposite to scalariform when present; perforation plates scalariform with 8–12 bars. *Rays* fairly distinctly of two widths; uniseriate of square to upright cells; multiseriate, 4–6 cells wide, with uniseriate margins of several rows of square to upright cells; maximum height up to 30 cells; vessel-ray pitting half-bordered with large rounded to elongated apertures and narrow border, often in scalariform arrangement; extraneous material scattered in individual cells of ray; crystals not observed. *Parenchyma* apotracheal, diffuse; crystal strands numerous. *Fibres* moderately thin-walled, with numerous distinctly bordered pits on radial and tangential walls; mean length 1·58 mm.

(iii) *Material.*—*V. rubifolia* (F. Muell.) Pamp., two (H) samples, eastern Australia; *V. serratifolia* Guill., one sample, New Caledonia.

(*t*) *Weinmannia*

(i) *General.*—This genus includes some 126 species of shrubs and generally small to medium-sized trees spread throughout the tropics of the southern hemisphere. The majority of species (78) occur in temperate and tropical South and Central America from Chile to Mexico; they are all small trees or shrubs confined to mountainous regions and are not of commercial importance as timber; the barks are said to be rich in tannin (Record and Hess 1943). Sixteen species occur in Madagascar and the Mascarene Islands, and the remainder in the south-west Pacific, chiefly New Guinea, the Philippines, and Fiji, extending to the Cook Islands and New Zealand. Some of the New Guinea species produce trees of commercial size but are found mainly at higher altitudes; the two New Zealand species are second storey trees of Podocarp rain forest and are not of commercial importance.

Material from seven species was available for examination; the wood of these is brown to reddish or pinkish brown with some slight lustre; texture fine and uniform; moderately light to moderately heavy; grain straight to somewhat wavy and interlocked; without odour or taste.

(ii) *Structure* (Plate 1, Fig. 5).—*Growth rings* indistinct. *Vessels* very small and invisible to small and indistinct to the naked eye; maximum tangential diameter 52 μ in *W. racemosa*, up to 132 μ in the remainder; mean member length 710–1290 μ; predominantly solitary (91–100 per cent.); evenly distributed; very numerous (up to 150/sq. mm in *W. racemosa*) to numerous (up to 30+/sq. mm in *W. ledermannii*); vessel pitting sparse, opposite to scalariform when present; diameter of borders 6–8 μ; perforation plates scalariform, generally with few (up to 6) and coarse bars, but fine and moderately numerous (up to 15) bars in *W. racemosa*; tyloses present in some samples; extraneous material sparse. *Rays* of two kinds but not always of two distinct widths; uniseriate, numerous, of square to upright cells; multiseriate 2–5 cells wide, mainly 2–4, with uniseriate margins up to 5 cells high of square and upright cells; maximum height variable from 20–35 cells; vessel-ray pitting coarse, half-bordered, often with wide aperture and appearing simple, rounded to elongated, but also in scalariform arrangement; crystals absent; extraneous material abundant. *Parenchyma* apotracheal, diffuse to diffuse-in-aggregate (sparse in one sample of *W. ledermannii*, tending to be associated with vessels, as well as sparse diffuse); crystal strands numerous; extraneous material abundant. *Fibres* moderately thin to thick-walled with small lumen, non-septate, with numerous distinctly bordered pits on radial and tangential walls; mean length 1·10–1·81 mm.

(iii) *Material.*—*W. blumei* Planch., two samples, Malaya and northern Sumatra; *W. ledermannii* Schltr., two samples, New Guinea; *W. racemosa* L.f., two samples, New Zealand; *W. serrata* Brongn. & Gris., one sample, New Caledonia; *W. silvicola* Soland., one sample, New Zealand; *W. simplicifolia* Merr., one sample, Celebes; *W. urdanatensis* Elmer, one sample, Molluccas; *Weinmannia* sp., aff. *W. urdanatensis*, one sample, New Guinea; *Weinmannia* sp., unassigned, one sample, Solomon Islands.

III. Summary of Anatomical Features

(a) *Cunoniaceae*

(i) *Growth rings* generally not evident or poorly defined, with the exception of *Anodopetalum*, where as well as being marked by denser fibres in the late wood, some samples show a ring of slightly larger vessels at the commencement of the growth ring.

(ii) *Vessels* generally solitary in the majority of genera, radial multiples predominating in *Aistopetalum*, *Anodopetalum*, *Ceratopetalum*, *Geissois*, *Pseudoweinmannia*, *Schizomeria*, and *Spiraeopsis*; evenly distributed throughout the family; somewhat variable in size between and within some genera, maximum tangential diameters from 50 μ in some species of *Pancheria* to 190 μ in one species of *Geissois*; few to extremely numerous (6–60+/sq. mm); mean length of vessel members from 670 μ in some species of *Codia* to 1580 μ in *Kaernbachia*, usually between 850 and 1250 μ; pitting usually alternate or loosely arranged in vessels with simple perforation plates (except in *Codia*) to opposite or scalariform in those with multiple perforation plates; perforation plates generally scalariform with few and coarse to many and fine bars up to 30 in number; simple in *Ceratopetalum, Codia, Schizomeria, Geissois, Aistopetalum, Spiraeopsis*, and *Pseudoweinmannia.*

(iii) *Rays* predominantly heterogeneous, at least in those genera with scalariform perforation plates, and often of two distinct widths; uniseriate of square to upright cells, and multiseriate 3–6 cells wide, occasionally up to 8 (*Kaernbachia*); (those genera with simple perforation plates and multiples of pores tend to have the less heterogeneous rays); maximum height generally less than 35 cells, up to 45 in *Kaernbachia*, *Gillbeea*, and *Opocunonia*; multiseriate generally with uniseriate margins of few to many rows of square or upright cells; vessel-ray pitting extremely uniform throughout the family, half-bordered with rounded to elongated aperture and narrow border and often in scalariform arrangement; this tendency is less marked in *Schizomeria* and *Ceratopetalum.* Crystals observed only in *Ceratopetalum, Schizomeria* p.p., and *Spiraeopsis*; usually very sparse.

(iv) *Parenchyma* predominantly apotracheal throughout the family (except in *Kaernbachia*); usually abundantly diffuse to diffuse-in-aggregate in fine, short, discontinuous lines, mostly uniseriate; *Ceratopetalum* has predominantly banded parenchyma; *Schizomeria*, *Cunonia*, and *Pancheria* have a tendency to banded or diffuse-in-aggregate as well as diffuse, the bands being 2–4 cells wide and often discontinuous; *Kaernbachia* is anomalous in having only paratracheal parenchyma; crystal strands and subdivided crystal-bearing cells in the parenchyma strands are a common feature throughout the family, with the exception of *Anodopetalum, Callicoma, Gillbeea*, and *Kaernbachia*; enlarged crystal-bearing cells composing part or sometimes the whole of strands common in *Ceratopetalum.*

(v) *Fibres* of two kinds in different genera:

1. "*Fibre tracheids*" generally thick-walled, non-septate, with numerous distinctly bordered pits on radial and tangential walls; mean length 1·21–2·5 mm.

2. *Libriform fibres* moderately thin to thick-walled, non-septate, with simple to indistinctly bordered pits, usually confined to the radial walls; mean length 1·16–1·64 mm.

Group 1 is confined to genera with solitary vessels and scalariform perforation plates (with the exception of *Codia*). In Group 2, *Ackama* and *Ceratopetalum* have some species with fibre pits having moderately distinct borders, but located mainly on the radial walls; these elements are difficult to assess as "libriform fibres" or "fibre tracheids" and are probably transitional in development.

(*b*) *Davidsoniaceae*

Davidsonia is a monotypic genus of one species and two varieties endemic to north-eastern Australia. The species produces small trees up to 30 ft high of no commercial importance as timber. The wood is red to red-brown and little paler towards the bark; moderately heavy to heavy; texture fine and uniform; grain straight; very slight lustre; without odour or taste.

(i) *Growth rings* distinct.

(ii) *Vessels* small and indistinct to the naked eye; maximum tangential diameter 90 μ; mean member length 810 μ; 60 per cent. solitary, the remainder in radial multiples up to 4, occasionally 5, and a few clusters; numerous (30+/sq. mm) (see Plate 5, Fig. 1); vessel pitting mainly opposite to scalariform but sometimes with a less marked opposite tendency; perforation plates both simple and scalariform with moderately fine bars; extraneous material abundant.

(iii) *Rays* 1–3, sometimes up to 4-seriate; up to 20 cells high, weakly heterogeneous with one or two squarish cells at margins; vessel-ray pits half-bordered, sometimes with large aperture, elongated and often scalariform in arrangement; crystals absent; extraneous material abundant.

(iv) *Parenchyma* apotracheal, diffuse to diffuse-in-aggregate; crystal strands numerous; extraneous material present.

(v) *Fibres* very thick-walled, lumen extremely small; non-septate, pits numerous on radial and tangential walls, with small but distinct borders: mean length 1·66 mm.

Material.—Davidsonia pruriens F. Muell., two samples eastern Australia.

(*c*) *Eucryphiaceae*

The genus *Eucryphia* occurs in the south of South America (two species), eastern Australia (one species), and Tasmania (two species), and produces small to moderately large trees from 40 to sometimes 120 ft high. *E. cordifolia* Cav. is found in Chile and Patagonia above 1500 ft altitude in mixture with *Myrceugenia* Berg. and *Nothofagus dombeyi* (Mirb.) Oerst, and at its best development produces trees up to 120 ft high and 2 ft in diameter. The timber is known as "ulmo" and is used for flooring, furniture, and vehicle framing (Record and Hess 1943). The species is only abundant south of the present extraction region and is, as yet, not common on the market. *E. glutinosa* (Poepp. & Endl.) Baillon is a small tree and not of commercial importance. The bark of both species is rich in tannin and that of the former species is used commercially. Two of the Australian species, *E. lucida* (Labill.) Baillon, leatherwood, and *E. moorei* F. Muell. are small to medium-sized trees and the timbers are not used to any extent, though they are tough and suitable for tool handles as well as for furniture and heavy construction. Samples from the two Australian species and one sample of *E. cordifolia* for comparison were available for examination. The heartwood of these is pale brown to pale pinkish brown; moderately light; texture fine and uniform; grain usually straight and fissile.

(i) *Growth rings* generally fairly distinct as bands of denser fibres in the late wood and distinguished by a somewhat marked diminution in size of pore in this region.

(ii) *Vessels* extremely small and invisible to the naked eye in *E. lucida* and *E. moorei*, and small and indistinct in *E. cordifolia*; maximum tangential diameters 60–90 μ; mean member lengths 1120–1370 μ; 55–75 per cent. solitary, the remainder in radial multiples of 2–3; very numerous (130–170/sq. mm) (see Plate 5, Figs. 2 and 3); pitting scalariform; perforation plates scalariform with 10–15 fine bars; spiral thickening present in all species examined (see Plate 5, Fig. 6).

(iii) *Rays* 1–2-seriate, weakly heterogeneous with 1 or 2 rows of square to sometimes upright cells on the margins; up to 30 cells high (see Plate 5, Fig. 4); vessel-ray pits half-bordered with wide apertures in scalariform arrangement (see Plate 5, Fig. 5); extraneous material present; crystals not observed.

(iv) *Parenchyma* apotracheal, diffuse, tending to be concentrated more in the later part of the growth ring.

(v) *Fibres* moderately thick-walled, non-septate; with distinctly bordered pits on radial and tangential walls; mean length 1·50–2·04 mm.

Material.—Eucryphia cordifolia Cav., one sample, Chile; *E. lucida* (Labill.) Baillon, 10 samples, Tasmania; *E. moorei* F. Muell., three samples, eastern Australia.

Examination of the genera *Cunonia*, *Belangera*, *Platylophus*, and *Weinmannia* with species occurring outside the area under consideration has revealed, in the case of *Cunonia* and *Weinmannia*, a structure essentially similar to species occurring in the south-west Pacific. The genus *Belangera*, occurring only in South America, is reported by Record and Hess (1943) to have septate fibres, and examination of one unassigned species of the genus has confirmed this; in other respects it resembles the genus *Geissois*, to which it is allied botanically. *Platylophus* has been described by Chalk and Chattaway (1935) and examination of available samples of this monotypic South African genus reveals a structure similar in fundamental features to *Davidsonia*.

IV. Discussion

A review of the anatomical features of the Cunoniaceae shows that there is no feature characteristic of the family, which is common to all genera, indicating that members of the family are at different levels of specialization. Thus the family as a whole can be readily separated into two distinct groups (Table 3).

The timbers of group I possess, in addition, mainly diffuse parenchyma, sometimes with a tendency to diffuse-in-aggregate; they are: *Spiraeanthemum*, *Opocunonia*, *Cunonia*, *Vesselowskya*, *Weinmannia*, *Pancheria*, *Callicoma*, and *Pullea*.

Kaernbachia, as pointed out in Section III, is anomalous in having paratracheal parenchyma, but otherwise is typical of group I. *Codia*, but for the fact that the perforation plates are simple, also belongs to this group.

The genera in group II, which includes *Aistopetalum*, *Anodopetalum*, *Ceratopetalum*, *Geissois*, *Schizomeria*, *Pseudoweinmannia*, and *Spiraeopsis*, are not so homogeneous as the genera in group I, and show varying levels of specialization. For instance, *Anodopetalum*, which is more advanced in its ray type than other genera of the Cunoniaceae, retains some scalariform perforation plates and opposite to scalariform vessel pitting; *Ceratopetalum*, though possessing opposite to scalariform vessel pits, has predominantly simple perforation plates; *Aistopetalum*, *Geissois*, and *Spiraeopsis* retain the more primitive type of ray, but are advanced in other characters.

Ackama and *Gillbeea* are intermediate between the two groups in having on the one hand fibres of the "libriform" type and vessels in radial multiples, and on the other, the more primitive heterogeneous ray and vessels with scalariform pitting and scalariform perforation plates.

In Table 4, the genera of the Cunoniaceae are listed according to the botanical classification of Engler. Such features as type of perforation plate, ray type, arrangement of vessels, and type of fibre have been chosen as it is considered that these indicate degree of specialization. It will be seen that the majority of genera at a lower level of specialization fall into Sections Cc, D, and E, and the more advanced into Sections A, Ca, and Cb. Section B contains genera at both higher and lower levels.

TABLE 3

CHARACTERISTICS OF THE TWO GROUPS IN THE CUNONIACEAE

Structure	Group I	Group II
Vessels	Predominantly to exclusively solitary	Commonly in radial multiples
Perforation plates	Scalariform	Simple
Pitting	Opposite to scalariform	Usually alternate or transitional
Rays	Markedly heterogeneous	Weakly heterogeneous
Fibres	With numerous distinctly bordered pits equally numerous on radial and tangential walls	With simple to indistinctly bordered pits, fewer on tangential than on the radial walls

In the previous review of the anatomy of the Australian genera of the Cunoniaceae, Dadswell and Eckersley (1938) have used distinctness of the borders of the fibre pits, together with intervascular pitting, as the major criteria in grouping the genera examined. This has led to the grouping of *Callicoma* with *Ceratopetalum* and *Anodopetalum*. In this paper, the genus *Callicoma* is considered as typical of the genera of group I, and the latter two genera, with the more advanced features of vessel multiples, simple perforation plates, and almost homogeneous to weakly heterogeneous rays, as more typical of group II, though both genera retain the opposite to scalariform vessel pitting.

In assessing the type of fibrous element encountered throughout the family, significance has been given in this paper, not only to distinctness of the pit border, but also to the number and distribution of the pits on tangential as well as radial walls. These criteria, taken in conjunction with the other features used in Table 5, give an assessment of the level of specialization of the various genera more in conformity with the botanical grouping.

The authors of the previous paper have pointed out the anomalous position of the species which was then referred to *Weinmannia lachnocarpa* F. Muell., suggesting that its structure conformed more closely to that of *Geissois*. This study has revealed that, though similar to *Geissois* in many respects, it differs from that genus in having weakly heterogeneous rays, whereas *Geissois* has rays that are markedly heterogeneous and of two distinct widths. However, it is distinct anatomically from *Weinmannia* and Engler has in fact placed it in the genus *Pseudoweinmannia* in his revision of the family.

TABLE 4

LEVELS OF SPECIALIZATION IN THE CUNONIACEAE, BASED ON WOOD ANATOMICAL FEATURES

Botanical Grouping of Genera	More Primitive Anatomical Features				More Advanced Anatomical Features			
	Perforation Plates Predominantly to Excl. Scalariform	Vessels Excl. Solitary	"Fibre Tracheids"	Rays Markedly Heterogeneous and Often of 2 Widths	Rays Weakly Heterogeneous	"Libriform Fibres"	Vessel Often in Radial Multiples	Perforation Plates Predominantly to Excl. Simple
	1	2	3	4	4*a*	3*a*	2*a*	1*a*
A.								
Geissois				+		+	+	+
Belangera				+		+ (septate)	+	+
B.								
Spiraeanthemum	+	+	+	+				
Aistopetalum				+		+	+	+
Kaernbachia	+	+	+	+				
Gillbeea	+			+		+	+	
C.								
Ackama	+			+		+	+	
Spiraeopsis				+		+	+	+
Schizomeria					+	+	+	+
a. *Ceratopetalum*					+	+	+	+
Anodopetalum	+/−				+	+	+	+/−
Opocunonia	+	+	+	+				
Platylophus	+/−		+		+		+	+/−
b. *Pseudoweinmannia*					+	+	+	+
Vesselowskya	+	+	+	+				
c. *Cunonia*	+	+	+	+				
Weinmannia	+	+	+	+				
D.								
Pancheria	+	+	+	+				
Callicoma	+	+	+	+				
Codia		+	+	+				+
E.								
Pullea	+	+	+	+				
Davidsonia	+/−		+		+		+	+/−

The genus *Davidsonia*, formerly included in the Cunoniaceae, resembles the monotypic genus *Platylophus*, though the percentage of solitary vessels is higher in some samples of the latter than in *Davidsonia*. The anatomical structure of this genus provides no evidence for its exclusion from the family.

The genus *Eucryphia*, although similar in many respects to *Anodopetalum*, can be readily distinguished from that genus, and the rest of the Cunoniaceae, by the presence of spiral thickenings in the vessels.

TABLE 5

GROUPING OF 19 GENERA OF THE CUNONIACEAE OCCURRING IN THE SOUTH-WEST PACIFIC AREA, BASED ON ANATOMICAL FEATURES

I. Vessels in radial multiples; perforation plates predominantly simple; fibres with indistinctly to sometimes distinctly bordered pits, mainly confined to the radial walls	
A. Rays weakly heterogeneous and not of two distinct widths	
1. Parenchyma diffuse to diffuse-in-aggregate, confined to outer part of growth ring	*Anodopetalum*
2. Parenchyma in regularly to irregularly spaced bands, sometimes discontinuous	*Ceratopetalum* *Schizomeria*
B. Rays markedly heterogeneous and of two distinct widths; parenchyma diffuse to diffuse-in-aggregate	*Aistopetalum* *Geissois* *Pseudoweinmannia* *Spiraeopsis*
II. Vessels frequently in radial multiples; perforation plates predominantly scalariform; fibres with indistinctly bordered pits, mainly on the radial walls	*Ackama* *Gillbeea*
III. Vessels predominantly to exclusively solitary; fibres with numerous distinctly bordered pits on all walls; rays markedly heterogeneous and usually of two distinct widths	
A. Perforation plates predominantly to exclusively simple ..	*Codia*
B. Perforation plates predominantly to exclusively scalariform	
1. Parenchyma paratracheal	*Kaernbachia*
2. Parenchyma diffuse, but often diffuse-in-aggregate in irregularly spaced tangential patches and loose concentric zones	*Cunonia*
3. Parenchyma diffuse to diffuse-in-aggregate in short, discontinuous tangential lines, 1 cell wide	*Callicoma* *Opocunonia* *Pancheria* *Pullea* *Spiraeanthemum* *Vesselowskya* *Weinmannia*

An artificial key to grouping of the 19 genera occurring in the area is set out in Table 5. No attempt has been made to distinguish between the genera in III B 3, as these genera vary less between themselves than is often the case between species of the same genus; *Callicoma*, however, is distinct from the remainder in the absence of crystal strands or crystal-bearing cells in the vertical parenchyma.

The genera of this Group III B 3 resemble, in many respects, genera of the Escalloniaceae, Dilleniaceae, and Theaceae, in possessing fibres with distinctly bordered pits on all walls, solitary vessels with scalariform perforation plates, markedly heterogeneous rays, apotracheal, diffuse to diffuse-in-aggregate parenchyma, and scalariform arrangement of vessel-ray pits. The family Escalloniaceae is considered by many taxonomists to be allied to the Cunoniaceae, and the anatomy of these genera bears out this relationship. Distinguishing features are, however, apparent; the perforation plates in the Escalloniaceae tend to be longer and more vertical and to consist of more numerous and finer bars than those in the Cunoniaceae; the vessel pitting, in almost all cases, is fine to moderately fine and generally opposite in arrangement, and the vessel-ray pits tend to be of the same type, and infrequently scalariform in arrangement. The Dilleniaceae (apart from those genera with simple perforation plates), i.e. *Dillenia* and *Hibbertia*, also have the same features in common with this group of the Cunoniaceae. In *Dillenia*, however, the rays are conspicuously high (frequently several millimetres to over 1 cm) and often up to 12 or 15 cells wide, and the cells of the multiseriate rays are generally composed of square or brick-shaped cells, frequently containing raphides, a feature not observed in the Cunoniaceae. The rays in *Hibbertia* are not so conspicuous as those of *Dillenia*, but inclusions in the form of silica or raphides are a characteristic feature. No silica has been observed or reported in the secondary wood of the Cunoniaceae. It is difficult to find any consistent features which distinguish this group from members of the Theaceae, and it is with this family that confusion most often arises. On the whole, the genera of the Theaceae, unlike the majority of this group of the Cunoniaceae, have little crystal-bearing parenchyma, though the genus *Schima* is an exception to this, and often has strands of enlarged crystal-bearing cells similar to those of *Ceratopetalum*. The only other crystaliferous genus is *Eurya*, and here the inclusions are in the form of specialized cells in the vertical parenchyma containing raphides. Bausch (1938) considers that this family is closely related to the Dilleniaceae.

The remainder of the genera of the Cunoniaceae are too varied to draw comparisons with other families and are sufficiently distinctive in themselves.

V. Acknowledgments

Material used in this survey was taken from the standard collection of the Division of Forest Products which includes authenticated specimens received on an exchange basis from forestry authorities in Malaysia. Special reference must be made to specimens of Indonesian timbers received through the courtesy of Dr. Meyer Drees, Director of the Forest Research Institute, Bogor; and to specimens of New Guinea timbers kindly made available by Mr. C. E. Lane-Poole, collected during his survey of that region in 1924; and to specimens from this area received from Mr. J. B. McAdam, Director of the Forests Department of the Papua-New Guinea Administration. Recent material received from this area has been collected and identified by Mr. J. S. Womersley, Chief, Division of Botany, Department of Forests, Lae.

The authors are especially indebted to Mons. P. Sarlin, Chef du Service des Eaux et Forêts who enabled one of the authors to collect a number of wood samples of several of the endemic New Caledonian genera which otherwise would not have been included in this study.

The authors wish to express their thanks to Miss Margaret Marfleet, who carried out much of the preliminary wood examination and took many of the photomicrographs.

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Explanation of Plates 1–5

Plate 1

Fig. 1.—*Anodopetalum biglandulosum* A. Cunn. Transverse section showing marked growth rings, tendency to ring-porosity, vessel size and distribution. × 25.

Fig. 2.—*Callicoma serratifolia* (R. Br.) Andr. Transverse section showing solitary vessels and rays of two distinct widths. × 25.

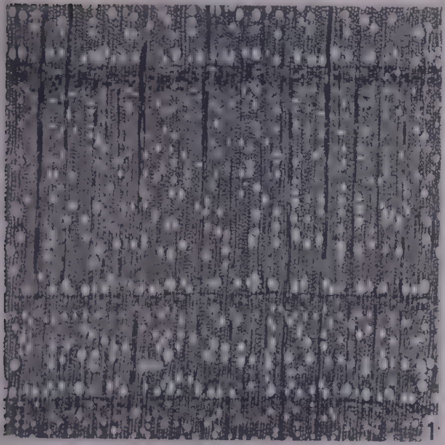
Fig. 3.—*Ackama paniculata* Engl. Transverse section showing vessel size and arrangement, and diffuse parenchyma. × 25.

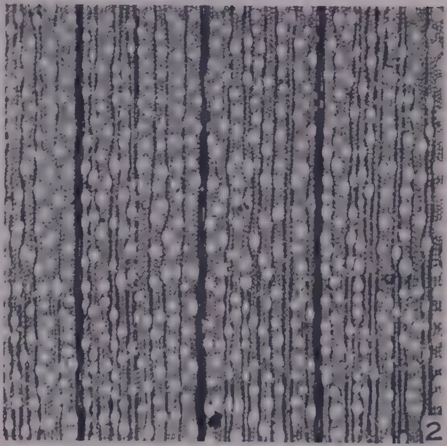
Fig. 4.—*Spiraeopsis glabrescens* Perry. Transverse section showing vessel multiples and clusters, and uniform width of ray. × 25.

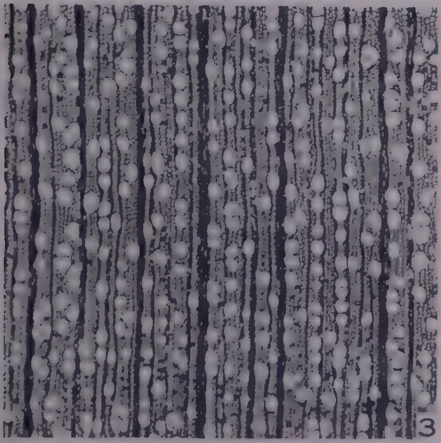
Fig. 5.—*Weinmannia silvicola* Soland. ex A. Cunn. Transverse section showing small, solitary vessels and diffuse parenchyma. × 25.

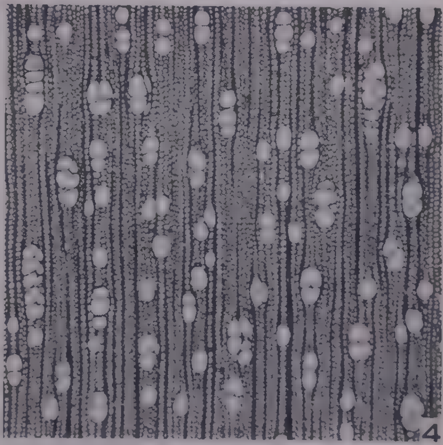
Fig. 6.—*Pullea glabra* Schltr. Transverse section showing solitary vessels and diffuse parenchyma. × 25.

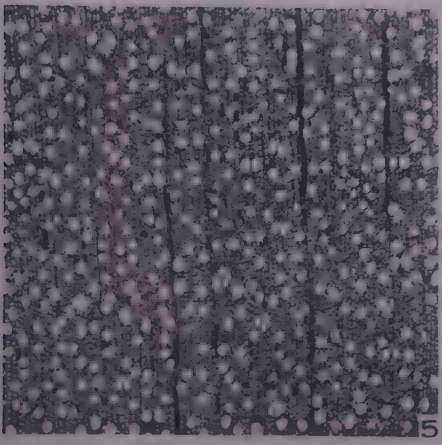
WOOD ANATOMY OF CUNONIACEAE, DAVIDSONIACEAE, EUCRYPHIACEAE

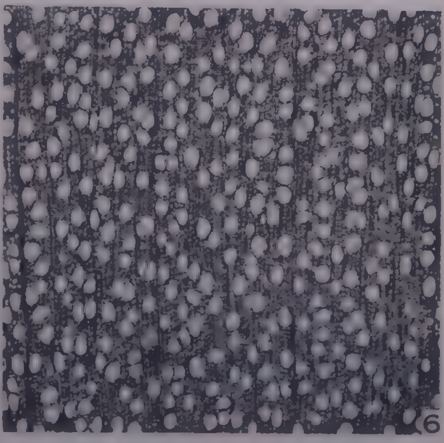












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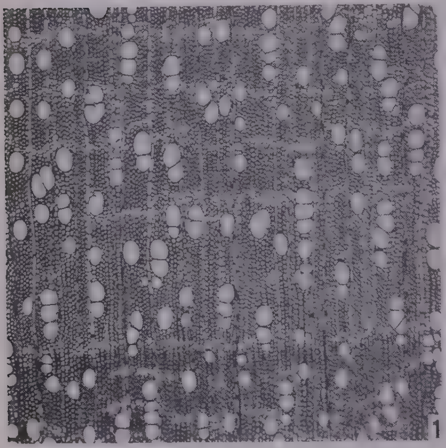
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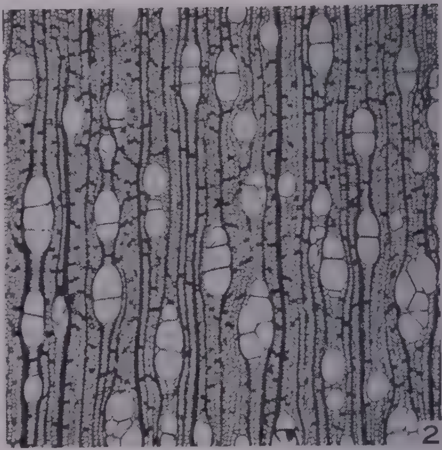
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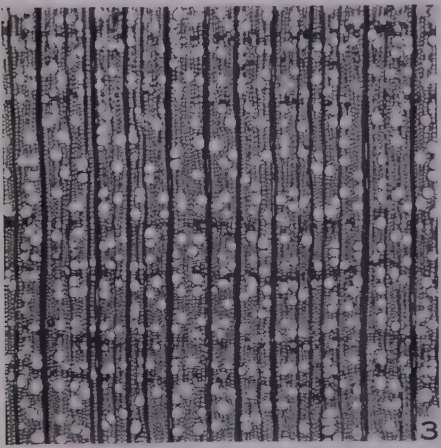
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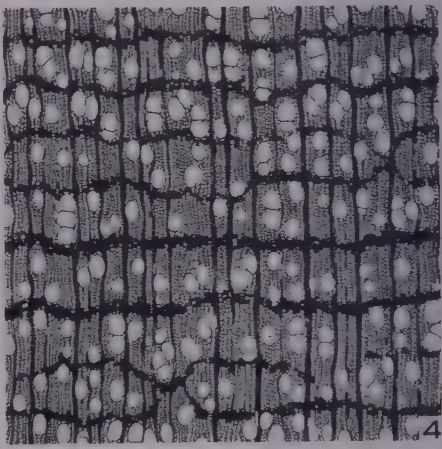
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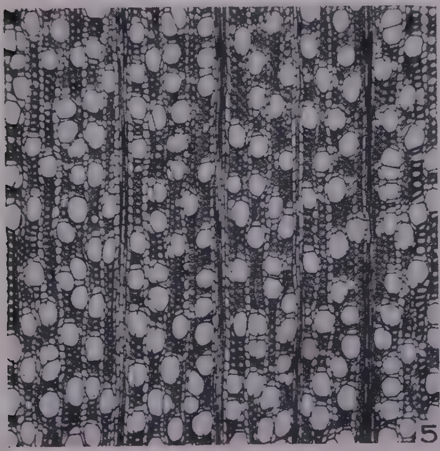
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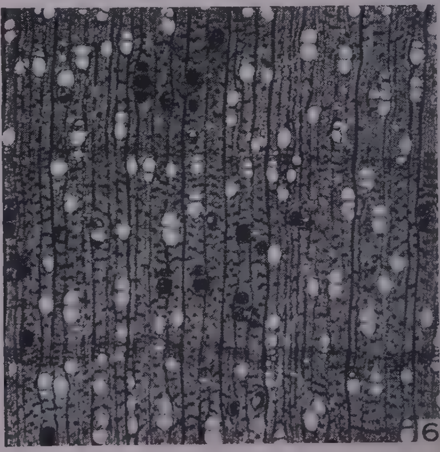
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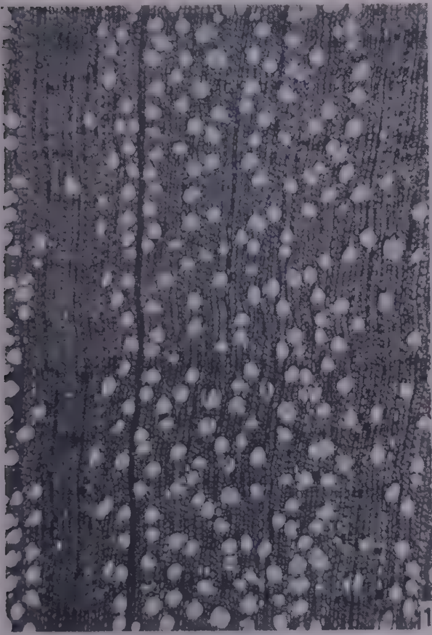
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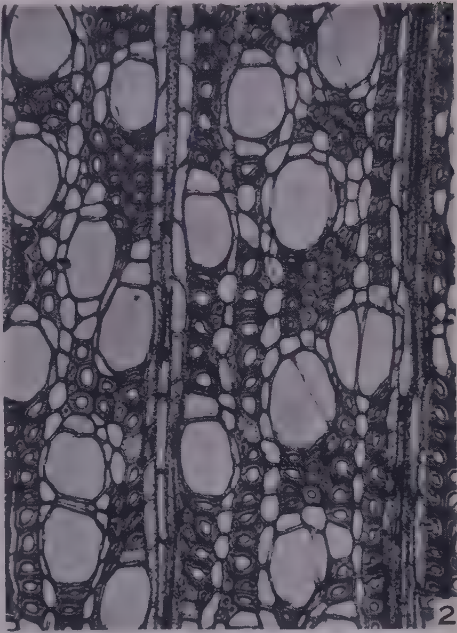
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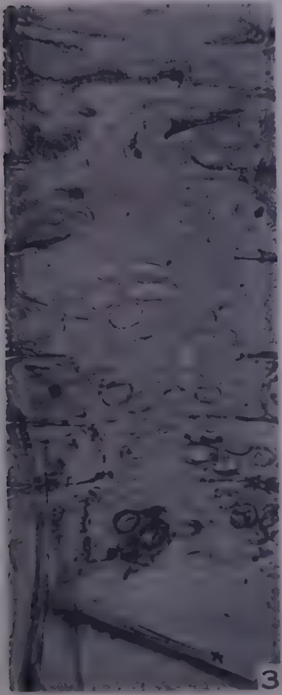
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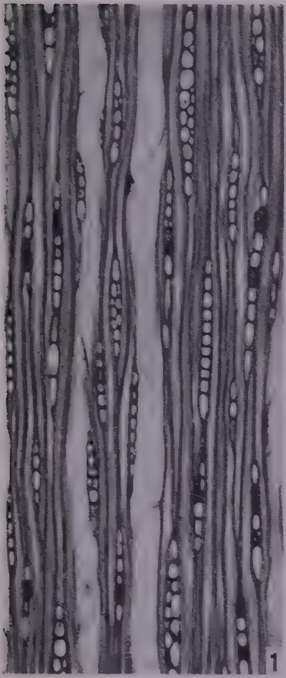
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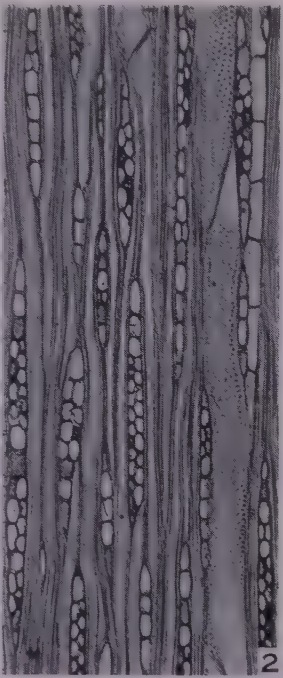
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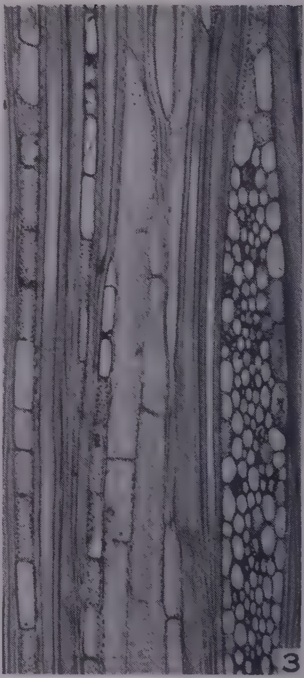
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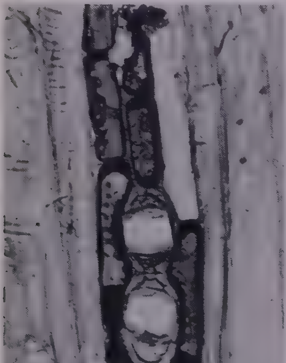
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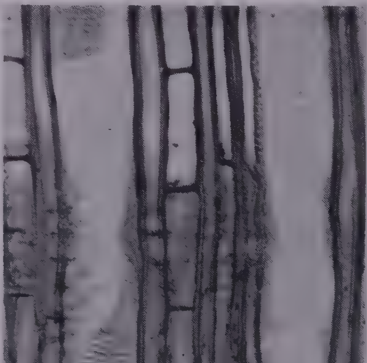
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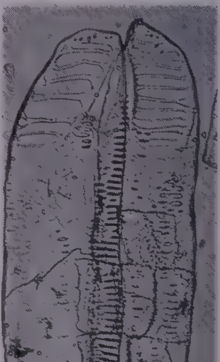
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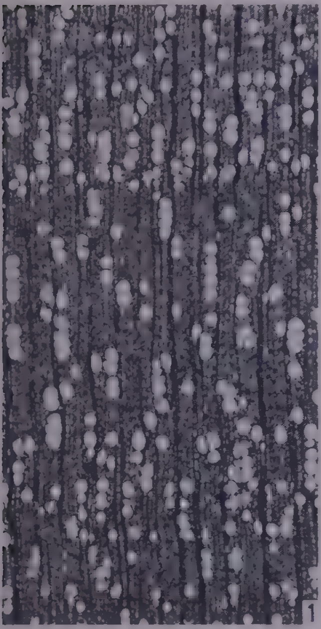
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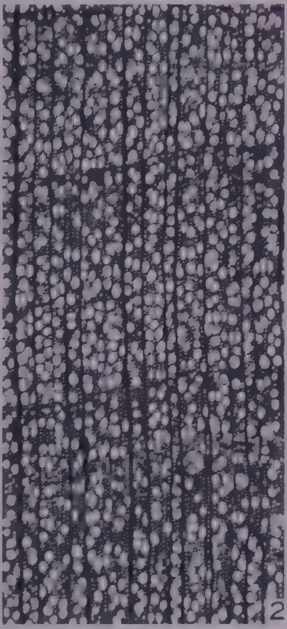
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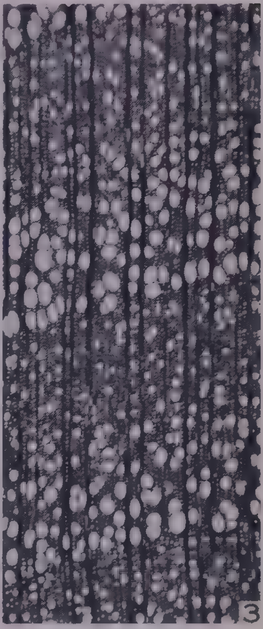
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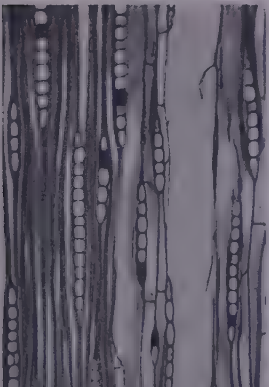
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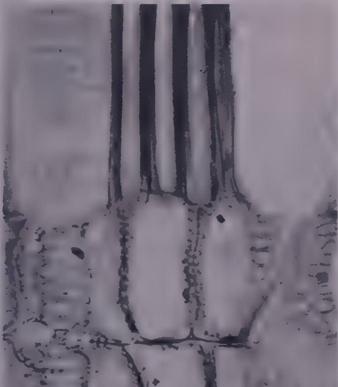
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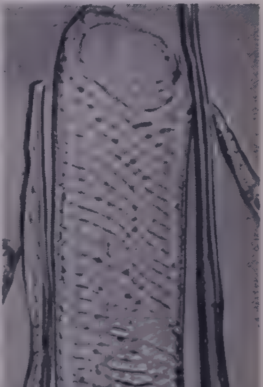
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Plate 2

Fig. 1.—*Schizomeria ovata* D. Don. Transverse section showing vessel multiples and irregularly spaced, discontinuous bands of parenchyma. × 25.

Fig. 2.—*Geissois biagiana* F. Muell. Transverse section showing vessel multiples and clusters, and diffuse-in-aggregate parenchyma. × 25.

Fig. 3.—*Ceratopetalum apetalum* D. Don. Transverse section showing parenchyma in irregularly spaced bands. × 25.

Fig. 4.—*Ceratopetalum succirubrum* C. T. White. Transverse section showing vessel size and arrangement, and bands of parenchyma. × 25.

Fig. 5.—*Kaernbachia pentandra* Schltr. Transverse section showing solitary vessels and paratracheal parenchyma. × 25.

Fig. 6.—*Pseudoweinmannia lachnocarpa* Engl. Transverse section showing vessels in multiples and diffuse to diffuse-in-aggregate parenchyma. × 25.

Plate 3

Fig. 1.—*Cunonia vieillardii* Brongn. & Gris. Transverse section showing radial segregation of vessels into alternating zones of few and more numerous vessels, giving a macroscopic appearance of aggregate rays. × 35.

Fig. 2.—*Kaernbachia pentandra* Schltr. Transverse section showing paratracheal parenchyma. × 90.

Fig. 3.—*Schizomeria ovata* D. Don. Radial longitudinal section showing vessel-ray pitting. × 400.

Fig. 4.—*Kaernbachia pentandra* Schltr. Radial section showing scalariform vessel-ray pitting. × 400.

Fig. 5.—*Spiraeopsis pubescens* Perry. Radial section showing characteristic vessel-ray pitting. × 400.

Plate 4

Fig. 1.—*Anodopetalum biglandulosum* A. Cunn. Tangential section showing advanced type of ray, homogeneous to weakly heterogeneous. × 90.

Fig. 2.—*Schizomeria ovata* D. Don. Tangential section showing weakly heterogeneous rays, uniseriate few and low. × 90.

Fig. 3.—*Kaernbachia pentandra* Schltr. Tangential section showing rays of two types, uniseriates numerous and high, multiseriate with tendency for sheath cells. × 90.

Fig. 4.—*Ceratopetalum apetalum* D. Don. Radial longitudinal section showing portion of a strand of enlarged crystal-bearing cells. × 180.

Fig. 5.—*Anodopetalum biglandulosum* A. Cunn. Radial section showing vessels with scalariform and simple perforation plates. × 180.

Fig. 6.—*Ackama australiensis* C. T. White. Vessel members from macerated material showing scalariform perforation plates and vessel-ray pitting. × 90.

Plate 5

Fig. 1.—*Davidsonia pruriens* F. Muell. Transverse section showing vessels in radial multiples and diffuse parenchyma. × 25.

Fig. 2.—*Eucryphia moorei* F. Muell. Transverse section showing very numerous small pores. × 25.

Fig. 3.—*Eucryphia cordifolia* Cav. Transverse section showing ring-porous tendency and aggregation of parenchyma in the later portion of the growth ring. × 25.

Fig. 4.—*Eucryphia lucida* (Labill.) Baillon. Tangential section showing uniseriate rays. × 25.

Fig. 5.—*Eucryphia lucida* (Labill.) Baillon. Radial section showing vessel-ray pitting. × 320.

Fig. 6.—*Eucryphia cordifolia* Cav. Vessel member from macerated material showing spiral thickening. × 200.

THE NATURE OF REACTION WOOD

V. THE DISTRIBUTION AND FORMATION OF TENSION WOOD IN SOME SPECIES OF EUCALYPTUS

By A. B. Wardrop*

[*Manuscript received March* 27, 1956]

Summary

The development of tension wood has been studied in various species of the genus *Eucalyptus* under a number of natural and experimental conditions. It is considered that the distribution of tension wood in the cases observed is consistent with the view that this tissue is an anatomical manifestation of various regulatory processes associated with the maintenance of tree form and movements of orientation in response to environmental changes. Experiments were performed which demonstrate that the development of tension wood is associated with contraction in the stem or branches and that the resulting movements of orientation result from forces developed during differentiation of the fibres and not as a result of differential osmotic effects in the cambium.

I. Introduction

The nature of the various intrinsic and environmental factors governing the development and distribution of reaction wood has been the subject of extensive investigation (Munch 1937-38; Jaccard 1938; Sinnot 1952). Apart from the work of Jaccard this study has generally been concerned with the development of compression wood of gymnosperms, although in many respects the arguments developed are in principle applicable to the development of tension wood in angiosperms.

In considering the earlier work on the development of reaction wood, three main points of view can be distinguished. These may be considered separately under (*a*), (*b*), and (*c*) below.

(*a*) *Tension Wood Development as a Stress Response*

In the examination of branches and leaning stems of angiosperms it was early recognized that tension wood occurs on their upper side. Further, if a stem were bent artificially then tension wood was observed to develop on the upper side (Fig. 1), i.e. the side placed in tension. This led to the view that tension wood was a morphological response to the presence of tensile stress in the branch or stem where this stress arose due to the weight of the branch, or was artificially induced (Fig. 1). Such a view was also consistent with other observations such as those of Vochting (see Wardlaw 1952) that the development of mechanical tissue in the petioles of pumpkins, which occurred when the fruit developed from hanging vines, was reduced or absent when the fruit developed on the ground. Similarly, it was reported by Haberlandt (1914) that tendrils which fail to grip a support do not develop mechanical tissue and atrophy. Again, the evidence of Rasdorsky (see Busgen and Munch 1929) showed that *Helianthus* stems, which were grown supported so that there was no pressure of the stem on its base, did not develop sufficient mechanical tissue to maintain the stem erect when the supports were removed.

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* Division of Forest Products, C.S.I.R.O., South Melbourne.

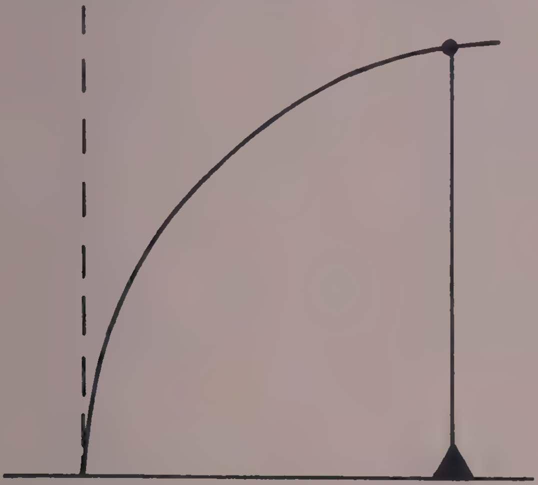

Fig. 1.—For explanation, see text.

Relevant also are the earlier experiments of Knight (see Wardlaw 1952) who observed that in stayed trees mechanical tissue developed to a greater extent in those regions of the stem exposed to mechanical action of the wind. These observations led to the view that the development of thick-walled mechanical tissue, of which tension wood is an outstanding example, is induced by the operation of stress in the organs in which this tissue is developed.

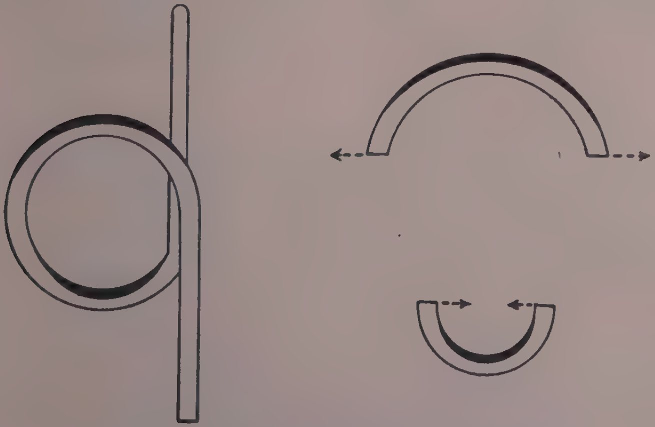

Fig. 2.—For explanation, see text (after Jaccard 1938).

(*b*) *The Development of Tension Wood as a Gravitational Response*

Inadequacies in the view that tension wood is a morphological response to stress alone became apparent in the experiments of Jaccard (1938) in which twigs were bent into vertical loops (Fig. 2) and tension wood developed on their upper side irrespective of whether these regions were placed in tension or compression. Similarly, in horizontal loops tension wood developed on the upper side (Jaccard 1938) so that it appeared that the particular morphological changes involved in the development of tension wood were primarily a geomorphic response. A further feature was recognized by Jaccard in that when vertical loops were sawn in half after growth had proceeded some time the upper chord of the loop expanded, whereas the lower chord contracted (Fig. 2). Taking into account the observed tension wood distribution it thus appeared that irrespective of the initial stress condition in the loop the development of tension wood tended to produce, or to be associated with, forces leading to the contraction of the stem. These and other similar experiments led Jaccard to the hypothesis that tension wood is involved in governing the orientation of branches and stems so that they acquire an equilibrium position in relation to gravity.

(*c*) *Tension Wood Development and Tree Form*

The idea of the existence of an equilibrium disposition of the stem and branches finds further development in the work of Hartmann quoted by Sinnot (1952). It was shown in this investigation that in conifers compression wood, which in contrast to tension wood normally forms on the lower side of branches and leaning stems, could be induced to form on the upper side of branches bent upwards towards the axis. According to Sinnot there is an inherited form or pattern of the shoot system which is genetically controlled and in the maintenance of which the development of reaction wood is involved. Whether these considerations apply in the case of tension wood will be discussed further below.

The concepts of Jaccard and of Hartmann that reaction wood is involved in "movements of orientation" (Jost 1907) of the branches and stems either in relation to gravity, variations in light, or other environmental influences, or as a mechanism in the maintenance of inherited characteristics of tree form, poses the further problem of the means by which such movements are brought about, and the way in which the development of tension wood is involved in association with them.

(*d*) *The Mechanism of Orientation Movements Associated with Tension Wood Formation*

The experiments on the development of tension wood in loops by Jaccard, already referred to, demonstrated the development of a contraction associated with tension wood formation. This contraction, it was suggested by Munch (1937-38) originates in the growth stresses of the stem. The origin of these stresses is to some extent obscure although Jacobs (1945) and Boyd (1950) have pointed out that they may arise in some change, probably in cell wall texture, associated with the differentiation of the fibres from the cambium. In symmetrical stems the centre is in compression relative to the periphery, and from a study of the stress distribution Jacobs has suggested that an asymmetrical development of the stem alone would bring about an asymmetrical distribution of growth stress which could effect movements of orientation of branches and stems. According to this view the development of tension wood as such does not form part of the mechanism of movements of orientation, although Jacobs has demonstrated that where tension wood is present the stress development is abnormally high.

A different view of the mechanism of orientation movements has been proposed by Frey-Wyssling (1952) for the case of stems undergoing response to gravity. He suggested that the origin of the force leading to bending of the stem lies in the cambium and that forces in excess of the normal osmotic pressure are involved. Frey-Wyssling pointed out that the bending of a growing stem does not correspond to the elastic bending of a rigid body but to the deformation or creep of a plastic body under long-time loading. On this basis he calculated that pressure generated in the cambium of the order of 50 atm would be necessary to effect the recovery of a conifer stem of 10 cm radius. He regarded the reaction wood as being produced by the stem to maintain the orientation achieved after bending as a result of osmotic and other forces arising in the cambium. He further pointed out that the cell wall organization of the tissue is particularly adapted for this purpose.

In the following discussion attention is directed to the distribution of tension wood in several species of *Eucalyptus* and to preliminary experiments relating to the various hypotheses of the mechanism of orientation movements discussed above. In the pale-coloured commercial species of *Eucalyptus* the occurrence of tension wood is fairly widespread and as previously stated (Wardrop and Dadswell 1948) associated with undesirable features of behaviour of the wood. A study of its distribution and development is thus of technological interest as well as of interest in relation to its anatomy and role in morphogenesis.

II. OBSERVATIONS AND DISCUSSION

One serious limitation in studies of tension wood formation is the relatively slow rate at which observations can be made. Accordingly, at the beginning of this study a survey was made to find material in which growth was rapid and in which easily recognized tension wood developed. For this purpose, young shoot material was examined. The most suitable material proved to be the very rapidly growing epicormic shoots of various species of *Eucalyptus*. Indeed, in this material it was almost impossible to find shoots which did not contain tension wood and by suitably bending or otherwise treating the shoots recognizable development of tension wood could be induced in 2–3 weeks. Many of the shoots grow in length by as much as 2–4 in. in one week. In view of these observations, most of the experiments here described were performed on epicormic shoots of *E. elaeophora* F. Muell. at Blackburn, Vic., or with young saplings of *E. goniocalyx* F. Muell. in the Toolangi district, Vic., a mountainous region about 50 miles east of Melbourne, as well as specimens of *E. cladocalyx* F. Muell. grown in a glass-house.

(*a*) *Evidence Relating to the Functional Significance of Tension Wood Formation*

In the introductory section of this paper reference was made to the idea advanced by Hartmann that development of reaction wood is associated with movements of orientation in the stem and branches governed by various genetically determined and environmental factors. In both naturally growing specimens and in experimental material evidence consistent with these views was obtained. In Plate 1, Figure 1, is shown an epicormic shoot of *E. elaeophora*. The orientation of this specimen at time of collection is shown in Figure 3. The shoot arose on the shaded side of the stump and then grew around the top of it until it acquired an equilibrium position in relation to light and other environmental influences. Sections were cut from the fresh material at a number of points and stained, using the safranin light green technique previously employed (Wardrop and Dadswell 1948). The distribution of tension wood at selected points on the shoot is shown in Figure 4.

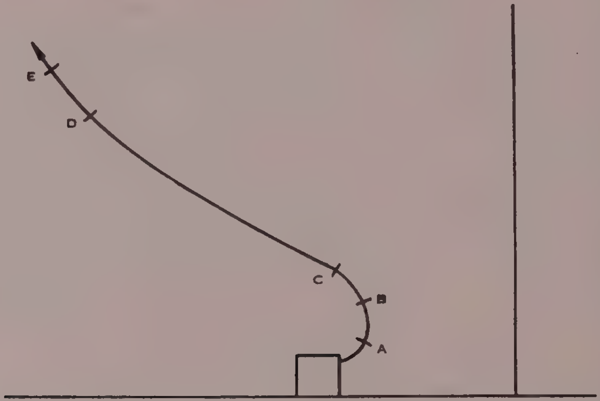

Fig. 3.—Diagrammatic representation of original orientation of the specimen shown in Plate 1, Figure 1. The epicormic shoot was shaded by a fence at right.

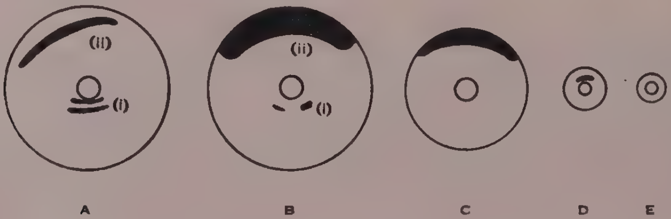

Fig. 4.—Showing the distribution of tension wood in the specimen shown in Figure 3 and Plate 1, Figure 1.

It can be seen that at points *A* and *B* the tension wood was present as a small arc near the pith and at *B* and *C* as a broad arc in the currently forming wood on the opposite side of the cross section. At point C only the broad arc was present, and at D and E tension wood was absent in the currently forming wood. From the difference in radial position of the arcs in sections A and B, it is clear that those nearer the pith were formed not only prior to those near the bark but at a time when the orientation of the shoot was quite different. Thus, if tension wood tends to bring about a contraction on that side of the shoot on which it is present (Section I and see below), then the arc (ii) (Fig. 4), is obviously associated with the tendency to become erect in the shoot at the time of its collection, whereas the inner arcs (i) were formed when the shoot was much shorter and was changing orientation in a direction different from that at the time of collection. Thus, soon after growth had commenced tension wood would presumably be formed on the upper side of the shoot but after further growth with the changed direction of the apex this side became the lower side and so the observed distribution could result.

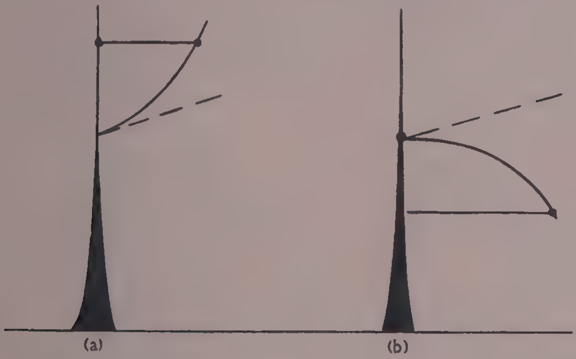

Fig. 5.—Induction of tension wood by bending branches towards the stem. The initial orientation of the branch is shown by the broken line.

In this case, the distribution of tension wood on both sides of the pith as seen in cross section can thus be attributed to the changing direction of the apex during growth.

In the wood formed early in the growth of the stem the tension wood distribution may well result from irregular growth as in the case of the shoot in Plate 1, Figure 1. In mature trees, however, the shifting location of the tension wood in the stems is more difficult to explain; but, accepting that the crown of the tree is growing and exerts a changing stress on the stem, it is reasonable to suppose that the arcs of tension wood formed represent a compensating growth in the stem to accommodate the changing load of the crown.

The suggestion that the development of tension wood is associated with growth movements involved in the maintenance of tree form was also supported by the results of another series of experiments.

Figures 5 (a) and 5 (b) show results of experiments similar to those carried out by Hartmann and Sinnot on gymnosperms (Sinnot 1952). In the experiment shown in Figure 5 (a) a branch was bent upwards out of its normal orientation, whereas in Figure 5 (*b*) a shoot was bent downwards out of its normal orientation. In the former case tension wood developed on the lower side of the shoot, whereas in the latter case development was on the upper side. If tension wood development is accepted as being associated with a tendency of the stem to contract, then these observations may be interpreted to mean that in each case the tension wood developed in a position which, if free to do so, would enable the branch to regain its initial orientation with respect to the axis.

The above series of observations are consistent with the view that tension wood development is associated with growth movements in stems or branches, whether these movements result from extrinsic or intrinsic factors.

The distribution of tension wood appears to be consistent with the view that it is developed in those regions of the stem where a contraction would form part of a process directed towards the realization of some inherited character (Fig. 5) or of some demand of the environment (Fig. 3). This may be seen as a case of general principle formulated by Russel (1945): "If . . . normal structural and functional relations either external or internal, are disturbed, activities will usually be set in train that are directive towards restoring structural and functional norms or establishing new norms which are adapted to the altered circumstances".

In a general way this view is also consistent with a series of observations made on the tension wood distribution in a young erect stem of *E. goniocalyx*. In this specimen no tension wood was observed in the currently forming wood of the stem, but was present in wood formed earlier when the stem was thinner and presumably more irregular in its habit of growth. In the branches, too, it was observed that immediately adjacent to the stem the currently forming wood was normal, but in wood formed earlier arcs of tension wood were present on their upper sides. At the tips of the branches tension wood was present, i.e. where growth movements of orientation were more likely to have been in progress at the time of collection of the specimen. Thus, the distribution of the tension wood is not simply a function of position in the branch or stem, but is formed, as Russel (1945) has pointed out in analagous cases, in response to a need.

(*b*) *Eccentric Growth and Tension Wood Formation*

Usually the development of tension wood results in eccentric growth on the side of the stem in which tension wood is formed. That this is not always so, however, has been indicated by Jaccard (1938) and in the present series of field observations a number of cases has been observed in which no eccentricity was apparent and occasionally a case was observed in which the eccentricity was opposite to the side on which the tension wood was formed. Furthermore, there has been a number of references in the literature (e.g. Chow 1946) to the question of the fibre length of tension wood as compared with normal wood. However, determinations of fibre length of tension wood have been conflicting, sometimes greater and sometimes smaller values being reported. In a recent survey by Dadswell and Wardrop (1955) it has been shown that the fibres may be greater, equal to, or less than those of normal wood. This question of fibre length is related to that of eccentric growth since in *E. gigantea* Hook. it has been demonstrated by Amos, Bisset, and Dadswell (1950) that the fibre length is inversely related to the radial growth rate. This gives rise to the question of the origin of eccentric radial growth in stems.

This could obviously arise from a differential rate of radial growth on the opposite sides of the stem or branch or from a differential time of radial growth. Accordingly, a series of field observations was undertaken to observe the initiation of cambial activity in stems and branches of various species of *Eucalyptus*. As a criterion of cambial activity the "slipping" of the cambium was used. When growth begins the bark separates easily from the wood (Priestly, Scott, and Malins 1933). This may not necessarily indicate an increase of cell division but probably represents the swelling or preparation of the cambium for division to occur. This is particularly apparent in deciduous species when slipping of the bark indicates the inception of spring growth.

In leaning stems, particularly those of the "sabre butt" type growing on sloping sites, slipping was observed on the upper side of the bend in the stem at a time when the bark could not be removed on the lower side. In branches the bark was frequently observed to slip freely on their upper sides where presumably tension wood was present, but this did not occur on their lower sides. Furthermore, it was frequently observed with vertical stems that slipping of the bark did not occur uniformly round the stem, but was active only in regions below branches in which slipping of the bark was already apparent. An extreme case of this is seen in the specimen shown in Plate 1, Figure 2. In the branch *A*, slipping was apparent. At *B*, slipping also took place; this was apparently related to the activity at *A*. Tension wood was apparent at the points marked *T*, but, whereas a section through the region *C* showed eccentricity on the lower side opposite to the tension wood, at *D* the eccentricity was on the side where tension wood was present. In all cases examined, there was evidence that the progress of slipping was basipetal in the stem or branch.

From these observations it was concluded that the eccentricity frequently associated with tension wood formation could arise from a differential time of growth of the cambium, as well as a differential rate of growth. If then, as the evidence suggests, eccentricity of radial growth is not necessarily associated with tension wood formation, then the variable results observed for fibre length of tension wood can be understood. If the stem is eccentric on the side on which tension wood is formed, and this eccentricity arises from a different time of growth, then the fibres may be of the same length or longer than those in corresponding normal wood, but if the eccentricity results from an increased rate of growth, then the tension wood fibres would be expected to be shorter than those of normal wood.

While the above observations relate particularly to the distribution of tension wood they give little information as to the way in which the development of this tissue is associated with movements of orientation, or to the mechanics by which these movements are brought about. These points are considered in the following sections.

(*c*) *Factors Influencing Tension Wood Formation*

Since the geotropic response of stems pulled out of their normal vertical orientation is clearly initiated in the apex, it is reasonable to suppose that in so far as tension wood is involved in this response then the development of this tissue is also under apical control. However, evidence relating to this point is in some respects conflicting.

In a stem treated as in Figure 1 the development of tension wood was rapid, e.g. in one group of young trees of *E. cladocalyx*, tension wood had formed all along the upper surface in 14 days, but in another no tension wood was present after 5 days. The course of recovery of the stem can, however, be followed by attaching a spring balance to the stem in place of the fixed support shown in Figure 1, using it to serve as a simple auxanometer (Jacobs 1939). The change in the balance reading with time for *E. cladocalyx* is shown in Figure 6, the balance being attached 41 cm from the apex. The initial decrease in the balance reading was due to a relaxation of stress in the stem. This decrease was followed by an increase in the reading as the tension wood developed. If two such balances were attached to the stem at increasing distances from the apex, then the course of the recovery was as shown in Figure 7. It can be seen that the minimum curve for the balance 31 cm (1, Fig. 7) from the apex is very slightly displaced later in time from that for the balance 52 cm from the apex (2, Fig. 7), suggesting that the basipetal progress of the response is very rapid—in this experiment about 9 mm/hr. The slower rate of recovery of the stem at the lowest point may result from the greater thickness and consequently greater resistance to bending of the stem at this point.

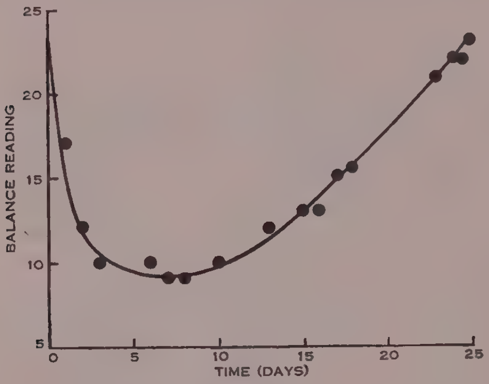

Fig. 6

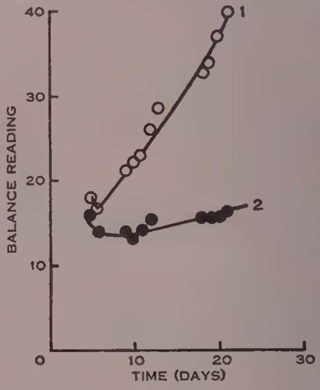

Fig. 7

Fig. 6.—Illustrating the course of recovery of a stem of *E. cladocalyx* bent into a horizontal position with a spring balance attached.

Fig. 7.—As Figure 6. Two balances were attached to the stem; (1) 31 cm from the apex, and (2) 52 cm from the apex.

It was observed further that after recovery of the stem had begun removal of the growing points did not inhibit recovery (Fig. 8). In this experiment the entire apex and unexpanded leaves were removed from each branch. This appeared to result in no change in the course of recovery of the stem and suggests that the presence of the apex is unnecessary for the continuance of recovery.

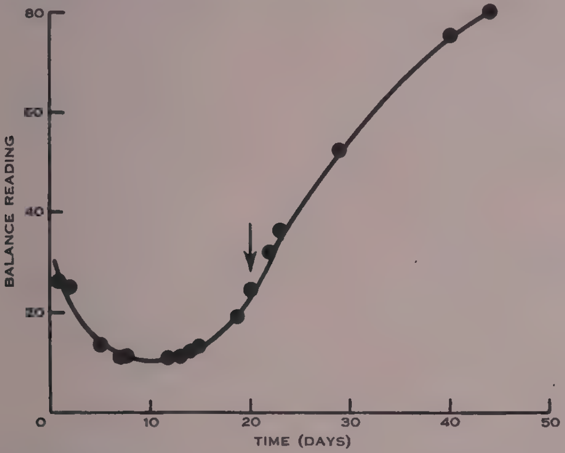

Fig. 8.—Illustrating the effect of removing the growing point on the course of recovery of a stem of *E. cladocalyx* bent into a horizontal position. The apex was removed at the time shown by the arrow.

On the other hand, young stems bent into the horizontal position (Fig. 1) after the removal of the apices from the stem and branches did not recover and tension wood did not form.

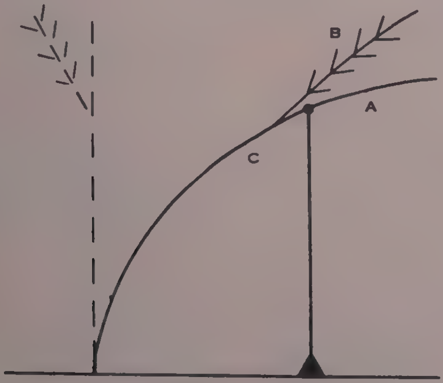

Fig. 9.—For explanation, see text.

A variation of this experiment is shown in Figure 9. A bifurcated stem was selected and the tip was removed from one branch, *A*, but not from the other, *B*. It was then bent into the position shown. After 40 days geotropic response took place in *B*, but not in *A*, and tension wood developed in *B* and at *C*. Thus the tension wood developed only in those regions of the stem directly associated with a growing point undergoing geotropic response. While it is obvious that no response will take place in the absence of an active growing point, the failure of tension wood to develop does suggest that the formation of this tissue depends initially on the response of the apex.

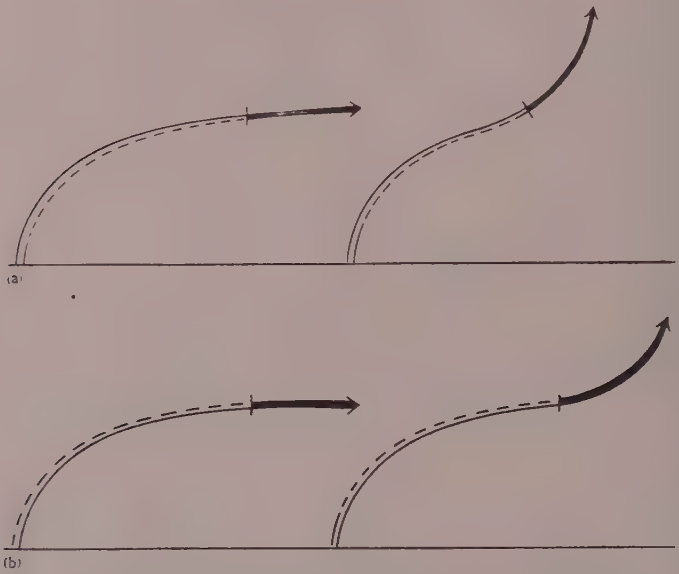

Fig. 10.—Diagrammatic representation of the effect of bark removal on the geotropic recovery of stems of *E. goniocalyx*. In (*a*) the bark was removed on the lower side (broken line) to a point below the apex. In (*b*) the bark was removed from the upper side.

It may be noted, however, that the failure of the removal of the apex to influence recovering stems (Fig. 8) may be related to the activation or development of epicormic shoots, the development of which was greatly enhanced in those species examined by bending the stem from its vertical orientation. Further examination of this point will be made in future investigations.

(*d*) *Movement in Stems and Branches and Tension Wood Formation*

In Section I reference was made to the idea of Jacobs (1945) that geotropic recovery could result from an asymmetrical distribution of growth stresses in leaning stems irrespective of tension wood formation, and that the force of contraction operating in the stem must arise during the changes associated with fibre differentiation. On the other hand, according to the more recent concept of Frey-Wyssling (1952) geotropic recovery results from a differential active uptake of water in the cambium on opposite sides of the stem resulting in a slow recovery of the stem.

In an attempt to examine these points further a series of experiments was designed as shown in Figures 10 (*a*) and 10 (*b*). In (*a*) bark was removed from the lower side of the stem along its length to a point near the apex. In (*b*) the stems were treated similarly but the bark was removed from the upper side. In each case the cambium was scraped free of partially differentiated tissue and covered with wool wax. In both cases the terminal region (i.e. the intact portion of the stems) showed positive response in a few weeks, in (*b*) this response did not proceed basipetally beyond the intact portion, but in (*a*) recovery gradually progressed down the stem. In (*a*) with the bark intact on the upper side characteristic tension wood developed. No tension wood developed in specimens of series (*b*), except in the intact portions of the stems.

In a parallel series of observations two young saplings of *E. goniocalyx* were treated similarly and were left for 6 months before collection. In these specimens, shown in Plate 2, similar results to those obtained with the epicormic shoots of *E. elaeophora* were obtained, but considerable regeneration of the stem had taken place. In the stems with bark removed from the lower side (Plate 2, Fig. 1), recovery had progressed downwards beyond the point of bark removal. Tension wood had formed along the length of most of the stem, and there was considerable formation of wound tissue proceeding basipetally, and laterally, as shown in Plate 3. When the bark was removed from the upper side (Plate 2, Fig. 2), although a considerable amount of wound tissue had formed, both basipetally and laterally, as shown in Plate 3, no recovery was apparent in the wound region. Here, however, after the initial formation of wound callus and the re-establishment of the cambium, tension wood was formed. In spite of this, recovery had not taken place presumably because the longitudinal development of the tissues had not progressed sufficiently. The type of wound response here established provides an interesting comparison with the work of Sharples and Gunnery (1933) with *Hibiscus*, in which a small piece of bark was removed from the stem without severe wounding of the underlying tissues; in this case normal stem callus developed over the whole wound surface, mainly from ray parenchyma. In this callus a new cambium was developed from which normal wood differentiated. In the cases described above, and shown in Plate 3, however, the underlying tissue was too severely wounded to permit callus formation from the partly differentiated wood and regeneration proceeded laterally from the edges of the wounded cambium. In other cases where the wound was even deeper so as to expose the pith, callus development took place also from the pith parenchyma. The examples shown in Plates 2 and 3 also suggest a tropistic influence in wound response as development of the wound tissue appeared greater on the upper than on the lower side (see Plate 3). This agrees with the observations of Brown (1937) and is consistent with the usually observed eccentricity of stem development associated with tension wood formation. That the wound tissue has the characteristic of tension wood, of course, simply reflects the operation of basipetally directed morphogenetic influences normally associated with tension wood formation.

Although the above experiments give no information as to the nature of the forces operative in the recovery of the stem, they appear to exclude the possibility that recovery involves a differential active uptake of water as suggested by Frey-Wyssling (1952) since, unless both sides of the stem were intact, it does not appear conceivable that such a mechanism could operate. Furthermore, it will be recalled from Figure 2 that Jaccard (1938) demonstrated with the aid of loop experiments that tension wood formation is associated with a tendency of the stem to contract. Since phenomena such as differential growth between the upper and lower sides of a stem are excluded in the present experiments, obviously recovery, as seen in the stems with bark removed from the lower side, means that contraction of the stem on the upper side must be involved.

In the above experiments asymmetry of the stem is artificially induced by wounding, a condition which usually arises by asymmetric stem development. If, then, it is assumed that asymmetry of growth stress distribution associated with tension wood formation is involved in the recovery of the stem, the question arises as to what factors give rise to the contraction on the upper side of the stem. Both Jacobs (1945) and Boyd (1950) have suggested that during differentiation of normal fibres there is a tendency of the cells to contract longitudinally. Jacobs has demonstrated that this tendency is enhanced in the case of tension wood.

Such a view is obviously in harmony with the occurrence of a contraction in the stem. Again, in stems such as that in Plate 2 in which bark was removed from the lower side, it is difficult to conceive of any active bending arising from osmotic forces, since the cells present on the upper side, being in active division, could reasonably be expected to be turgid. The fine structure of the fully differentiated fibres also showed evidence that bending had taken place. This could be seen in the presence of numerous slip planes and minute compression failures in a radial longitudinal section through the region of recovery in the specimen shown in Plate 2, Figure 1. These deformations are known to arise in bending tests in specimens under long-time loading, and, because of the axial orientation of the microfibrils in the unlignified or gelatinous layer of tension wood fibres (Wardrop and Dadswell 1948, 1953), they are readily induced in these cells. It is not suggested that these deformations arise at differentiation of the fibres but that they are induced in mature fibres by forces generated during differentiation of fibres less mature.

The question thus arises as to the possible sources of contractile forces. This has been explained by Munch (1937-38) in terms of the helical organization of the cell wall, the assumption being made that a pressure exerted by the gelatinous layer on the outer layer would result in a tendency towards cell contraction. However, any view which visualizes a cell as a closed body, so that a lateral expansion during differentiation would involve longitudinal contraction, does not appear consistent with present views of cell wall formation. Thus, it is known that differentiation from the cambium involves an increase in both length and breadth of the differentiating fibres and tracheids, and that increase in length proceeds by polar or bipolar tip growth. This length increase occurs simultaneously with radial expansion of the cells and may continue even after secondary thickening begins near the middle of the cells (Wardrop and Dadswell 1953). Obviously, during the period of these dimensional changes the intercellular region must be extremely plastic, and, since geotropic recovery can take place in the absence of differential osmotic effects, then the force governing recovery must arise during the period of secondary wall formation, and when the intercellular layer possesses a rigidity such that stresses generated can be transmitted to the mature xylem. Irrespective of the degree of development of the tertiary layer of the cell wall the most striking feature of tension wood is its low degree of lignification. This is paralleled in the tertiary layer by a high degree of crystallinity of the cellulose (Wardrop and Dadswell 1955). The question thus arises as to whether this difference in the physical texture of the cell wall is possibly related to the process of contraction which takes place. The existence of slip planes in all but the most recently formed tension wood fibres suggests that the contractile force must arise during the development of the cell wall. It is now recognized (Frey-Wyssling 1954; Wardrop 1954) that the microfibrils are surrounded by a paracrystalline phase of cellulose and that such a phase also surrounds the irregular crystalline areas or micelles within the microfibrils. It has been suggested by Berkley and Kerr (1946) that in cotton cellulose is first present entirely in the paracrystalline condition, and, although the evidence presented in support of such a view has been open to some criticism (Preston and Wardrop 1949), the suggestion has not been disproved. More recent unpublished work in this laboratory has also indicated the presence of entirely paracrystalline cellulose in the test of tunicates before drying. If cellulose is initially deposited wholly or partly in this condition then it is reasonable to assume that subsequent crystallization would involve a contraction in volume and it is suggested that this phase of crystallization may be the source of the contractile forces generated during differentiation. In general the crystallinity of cellulose seems highest when the lignin content is low and it may be that crystallization is facilitated by the absence of lignin. Such a hypothesis remains to be proved, since it has been shown in this laboratory (unpublished data) that the cellulose of fresh undried tension wood is highly crystalline although this in itself does not preclude the possibility that contraction takes place as a result of crystallization of the cellulose.

III. Conclusions

From the above discussion it can be seen that the formation of tension wood produces strong contractile forces capable of causing orientation movements in stems and branches. This contraction may arise from forces associated with the differentiation of the fibre cell wall. The distribution of tension wood in stems and branches under natural and experimental conditions seems consistent with the idea that this tissue is an anatomical manifestation of various correlative processes operating in the plant in response to both intrinsic and environmental influences.

IV. Acknowledgments

The author is indebted to Misses M. Day and I. Cairns for assistance in the course of the investigations and to Dr. H. E. Dadswell for helpful discussion.

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EXPLANATION OF PLATES 1-3

PLATE 1

Fig. 1.—*Eucalyptus elaeophora*—An epicormic shoot used to study tension wood distribution; see also text Figures 3 and 4.

Fig. 2.—*E. goniocalyx*—The upper part of a sapling used to study tension wood distribution (see text).

PLATE 2

Fig. 1.—*E. goniocalyx*—A sapling photographed after bending into the horizontal position for 6 months with the bark removed on the lower side. The bark was removed below the point *A*. *B* was the point of attachment of the anchoring wire. The arrow indicates the vertical position.

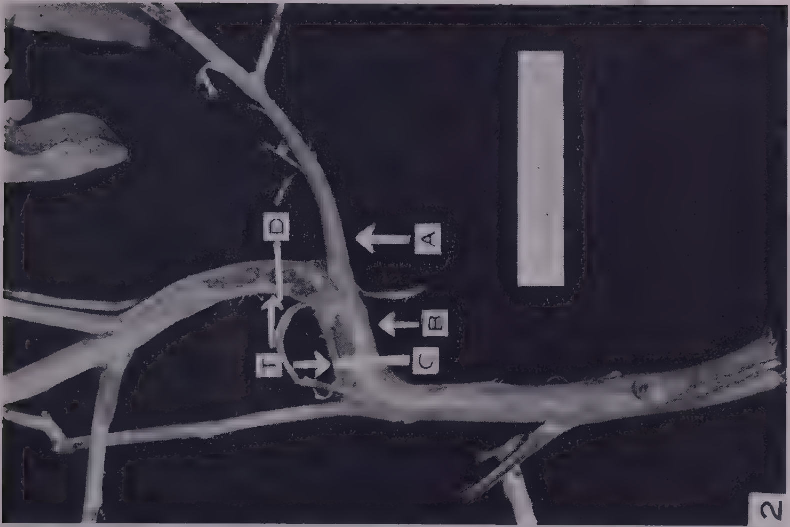
Fig. 2.—*E. goniocalyx*—A sapling photographed after bending into a horizontal position for 6 months with bark removed on the upper side. The bark was removed below the point *A*. *B* was the point of attachment of the anchoring wire. The arrow indicates the vertical position.

PLATE 3

Figs. 1-3.—Transverse sections of the stem shown in Plate 2 Figure 1. Figure 1 above the point of bark removal, Figures 2 and 3 below the point of bark removal. The tension wood is apparent on the upper side of the stem. × 4·3.

Figs. 4 and 5.—Transverse sections of the stem shown in Plate 2, Figure 2. Figure 4 above the point of bark removal; Figure 5 below the point of bark removal. Note the tension wood in the wound tissue of Figure 5. × 4·3.

NATURE OF REACTION WOOD. V



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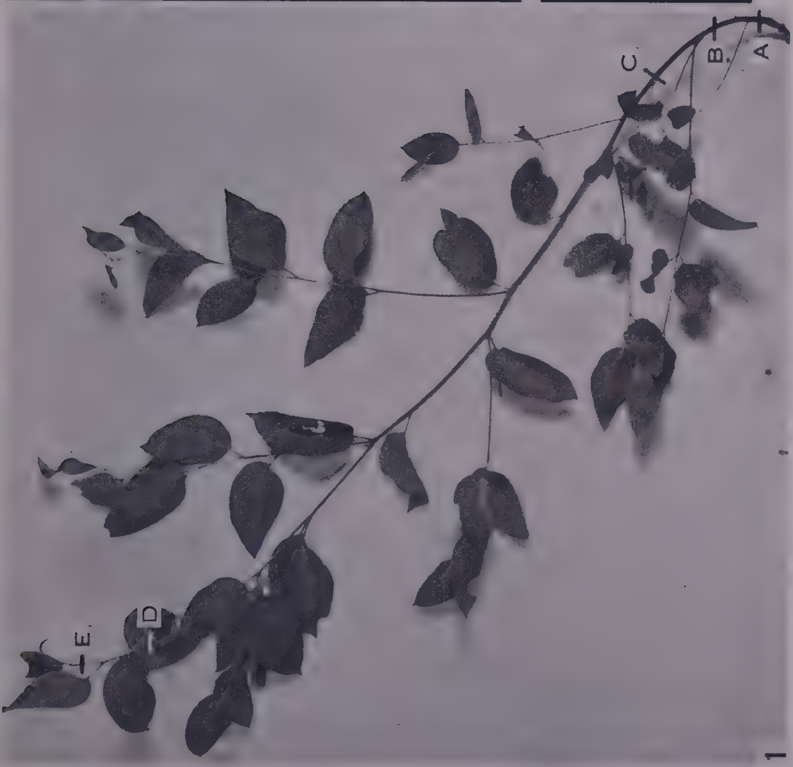

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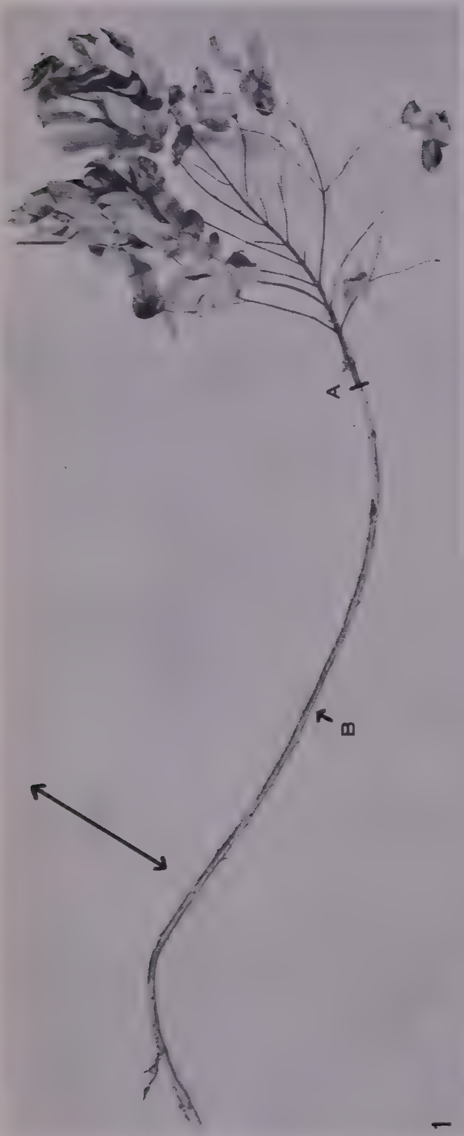

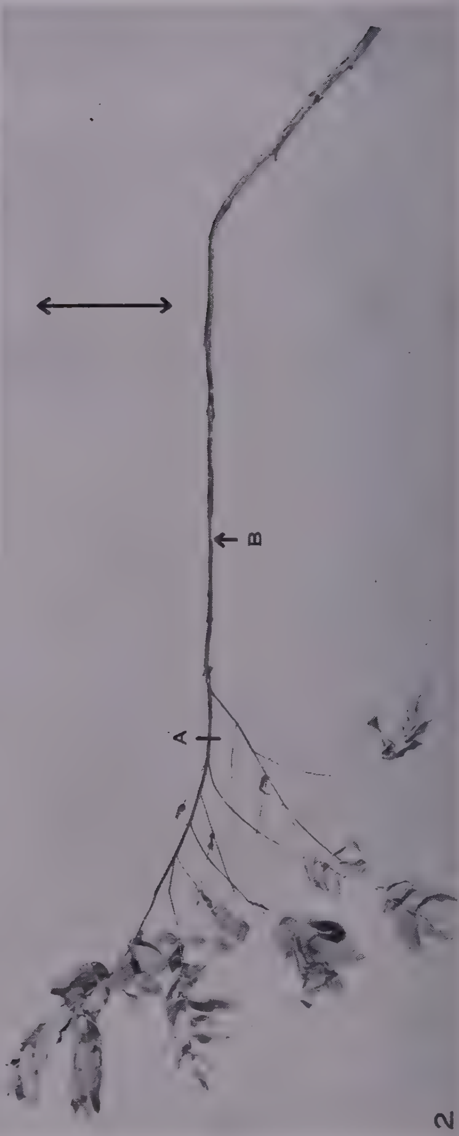

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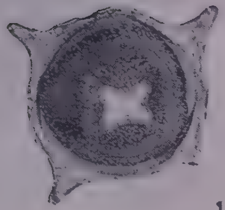
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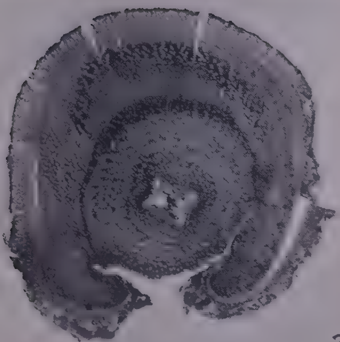
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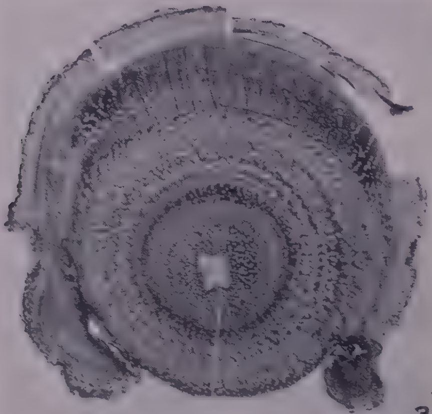
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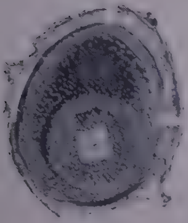
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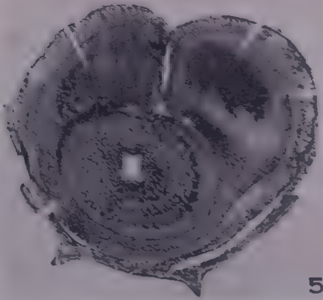
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THE ANALYSIS OF POINT QUADRAT DATA

By C. D. Kemp* and Adrienne W. Kemp*

[*Manuscript received November 22, 1955*]

Summary

The type of distribution followed by point quadrat percentage-cover data has been studied. The hypergeometric type IIA distribution with constant n has been deduced from theoretical considerations and found to give a good fit to data published by Goodall in 1952.

The parameters of this distribution assist the study not only of the overall percentage cover but also of the patchiness of the vegetation.

The assumption of this type of distribution does not preclude the use of the angular transformation; this remains the appropriate transformation for stabilizing the variance.

Theoretical considerations have been put forward in support of the policy of reducing the number of pins per frame. However, if this is done, the number of necessary locations is increased; only by practical experimentation can the optimum number of pins per frame be determined.

I. Introduction

The point quadrat method of estimating percentage cover has been discussed in considerable detail by Goodall (1952). He showed that (as previously suggested by Blackman (1935)) the probability of hitting a given species will vary less between the different sections of one frame than between different positions of the frame. If the expected proportion of contacts were constant for all locations of the frame the number of contacts per frame would be distributed as a positive binomial. However, vegetation studied by this method often shows considerable patchiness and the data obtained cannot usually be fitted by the positive binomial (Goodall 1952), the variance usually being too high. If the expected proportion of contacts is not constant from location to location, then the observed data will have a greater variance than can be accounted for by the positive binomial distribution. Recent work by Winkworth (1955) supports these findings.

Robinson (1954), in his study of area quadrats, has suggested that the fractional ground area covered by a particular species could be expected to follow the Pearson type I distribution (this distribution is better known as the Beta distribution). This is a simple distribution, yet it is flexible in shape. It is continuous and unimodal, gives all values from 0 to 1 and seems a reasonable choice for the distribution of the expected proportion of contacts from location to location.

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II. The Expected Frequency of Contact

Suppose then that the proportion is constant within a frame but has a Beta distribution between frames. The combination of Beta $(l, m; p)$* with the positive binomial (n, p) gives

$$P(r) = \binom{n}{r} \frac{\beta(l+r,\ m+n-r)}{\beta(l,\ m)}, \qquad r = 0, 1, \ldots, n,$$

where $P(r)$ is the probability of obtaining r contacts per frame of n pins. This result is equivalent to

$$P(r) = \binom{-l}{r}\binom{-m}{n-r} \bigg/ \binom{-l-m}{n}, \qquad r = 0,\ 1,\ \ldots,\ n,$$

which is the special case of the hypergeometric type IIA distribution (Kemp and Kemp 1956), where n is known. The limiting form of type IIA where l and m become infinite corresponds to the case where the expected proportion of contacts is constant and is, of course, the positive binomial. Taking the ratio of the variance to the mean as a measure of dispersion relative to the Poisson distribution, the hypergeometric type IIA distribution may be either over- or under-dispersed.

Skellam (1948) discussed this particular distribution and gave both moment and maximum likelihood solutions for estimating the parameters from observed data. More detailed forms of these are given in Appendix I. The method of moments provides a simple initial estimation which may then be improved, if desired, by successive cycles of maximum likelihood iteration.

Once the parameters have been estimated the expected frequencies of contact may be calculated by multiplying the probabilities given above by the total number of throws. Details are given in Appendix I.

III. The Meaning of the Parameters

The moment and maximum likelihood formulae are given in terms of l and m. However, as far as practical interpretation is concerned, the following parameters have more meaning:

$$j = \frac{l}{l+m},$$

$$k = \frac{lm}{(l+m)^2\,(l+m+1)}.$$

These are the mean and variance of the Beta distribution and, as such, measure the overall expected proportion and the amount of variation about this overall proportion from location to location.

$$* \ B(l, m; p)\mathrm{d}p = \frac{1}{\beta(l, m)}\, p^{l-1}(1-p)^{m-1}\mathrm{d}p, \qquad l, m > 0$$

where

$$\beta(a, b) = \int_0^1 x^{a-1}(1-x)^{b-1}\, \mathrm{d}x = \frac{\Gamma(a)\,\Gamma(b)}{\Gamma(a+b)}.$$

Assuming that the expected proportion of contacts has this variability from frame to frame we have:

Mean number of contacts per frame $= nj$,

Variance of number of contacts per frame $= nj(1-j)+n(n-1)k$.

Hence $n(n-1)k$ measures the variance in excess of that which would be expected on a positive binomial (constant expected proportion) assumption. This is the basis of the method given in Appendix I for calculating j and k for an observed set of data.

Point quadrat data have been used to some considerable extent to measure changes in percentage cover of particular species. Little use seems to have been made of this type of data in assessing changes in patchiness of the vegetation. Investigation of changes in the parameter k would enable us to do this. For instance, a situation of apparently stable conditions might arise in which there is no change in overall percentage cover (i.e. j remains constant), although the vegetation is becoming considerably less homogeneous (i.e. k is increasing).

IV. The Angular Transformation of Percentage Cover

When analysing percentage cover data it has become customary to use the angular (i.e. arc sine) transformation in an endeavour to stabilize the variance. This would be the appropriate procedure under the positive binomial assumption where the relationship between variance and mean is

$$V = M(1-M/n) .$$

It remains the appropriate transformation for stabilizing the variance under the hypergeometric type IIA assumption since the corresponding relationship merely involves an additional factor:

$$V = M\left(1-\frac{M}{n}\right)\left(\frac{l+m+n}{l+m+1}\right) .$$

V. The Number of Pins Per Frame

This relationship between variance and mean enables us to draw some conclusions concerning the number of pins per frame. Goodall (1952) has demonstrated that if the expected proportion of contacts is not constant from location to location then, for a given degree of precision, fewer pin observations have to be made if the frame consists of one pin rather than the customary ten. In general, if the number of pins per frame is decreased then the total number of pin observations needed is reduced.

Taking $M = nj$, the variance of a percentage cover value estimated from N_n throws of a frame of n pins is

$$V = \frac{j(1-j)}{N_n n}\left(\frac{l+m+n}{l+m+1}\right) \times 10000 .$$

Hence the necessary number of throws of a frame with a given number of pins may be found for any desired degree of precision.

TABLE 1

FREQUENCY OF CONTACT WITH PINS OBSERVED IN 200 FRAMES OF 10 PINS, COMPARED WITH EXPECTATION ON A HYPERGEOMETRIC TYPE IIA DISTRIBUTION

	Frequencies									
r	*Carex hebes* Nelnes		*Poa caespitosa* G. Forst.		*Rumex acetosella* L.		*Viola betonicifolia* Smith		*Asperula gunnii* Hook. f.	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
0	0	0·2	115	113·8	95	93·0	60	58·1	176	175·6
1	3	0·9	41	44·8	43	49·7	56	60·6	6	10·4
2	3	2·4	22	21·7	31	27·7	42	41·7	6	5·0
3	3	5·0	14	10·7	16	15·1	28	22·9	4	3·0
4	3	8·8	4	5·2	11	7·9	9	10·6	4	2·0
5	14	14·1	4	2·3	2	3·9	2	4·2	3	1·4
6	25	20·7	0	1·0	1	1·7	3	1·4	1	1·0
7	35	28·3	0	0·4	1	0·7	0	0·4	0	0·7
8	33	36·1	0	0·1	0	0·2	0	0·1	0	0·5
9	38	42·1	0	0·0	0	0·1	0	0·0	0	0·3
10	43	41·4	0	0·0	0	0·0	0	0·0	0	0·1
M, V	7·655, 4·126		0·815, 1·431		1·100, 1·900		1·440, 1·816		0·335, 1·093	
l_1, m_1	4·54, 1·39		0·72, 8·15		0·94, 7·62		2·59, 15·41		0·09, 2·70	
l^*, m^*	4·468, 1·371		0·640, 7·250		0·850, 6·910		2·478, 14·741		0·065, 2·008	
χ^2	$\chi^2_{[5]} = 7{\cdot}06$		$\chi^2_{[2]} = 1{\cdot}47$		$\chi^2_{[3]} = 3{\cdot}63$		$\chi^2_{[3]} = 1{\cdot}99$		$\chi^2_{[1]} = 3{\cdot}06$	

l_1 and m_1 are estimated by the method of moments.

l^* and m^* are the maximum likelihood estimates.

For the data published by Goodall in 1952 and further investigated in Section VI, it can be shown by this method that about 1000 locations of a frame with 1 pin or 300 locations of a frame with 5 pins (1500 pin observations) are equivalent to 200 locations of a frame with 10 pins (2000 pin observations). These results are in general agreement with those found by Goodall. However, it is important to realize that although, for example, 300 locations of a frame with 5 pins would involve 500 less pin observations than 200 locations of a frame with 10 pins, it would involve 100 more movements from location to location. Until the time saved in taking less observations and the extra time needed in taking more locations are found experimentally, it is impossible to decide which procedure would be more economical.

TABLE 2

MOMENT ESTIMATES OF nj AND $n(n-1)k$ FOR THE FIVE SPECIES

Species	nj	$n(n-1)k$
C. hebes	7·7	2·3
P. caespitosa	0·8	0·7
R. acetosella	1·1	0·9
V. betonicifolia	1·4	0·6
A. gunnii	0·3	0·8

TABLE 3

ESTIMATED NUMBERS OF LOCATIONS AND PIN OBSERVATIONS, FOR DIFFERING NUMBERS OF PINS PER FRAME, REQUIRED TO GIVE THE SAME PRECISION AS 200 THROWS OF A FRAME OF 10 PINS

Species	5 Pins per Frame		2 Pins per Frame		1 Pin per Frame
	No. of Locations	No. of Pin Observations	No. of Locations	No. of Pin Observations	No. of Locations (= No. of Pin Observations)
C. hebes	274	1370	495	990	864
P. caespitosa	288	1440	553	1106	994
R. acetosella	287	1435	550	1100	986
V. betonicifolia	327	1635	706	1412	1339
A. gunnii	234	1170	337	674	509

A further point to remember is that unless the frame consists of at least two pins it will not be possible to estimate patchiness by comparing within-frame variability with between-frame variability.

VI. EXAMPLES

For illustration, parameters were fitted by both the method of moments and the maximum likelihood method to data published by Goodall in 1952. Using the maximum likelihood estimates, the expected values were calculated and these are given together with the original data in Table 1. *Carex hebes* is here a dominant species comprising about three quarters of the sward. Its distribution appears to be quite unlike a Poisson or indeed any distribution, such as the negative binomial or Neyman's contagious distributions, where r can take values greater than n $(= 10$ in these examples). This objection is not so important for the other species which all have much lower means.

All species showed good agreement between the observed frequencies and those expected on the hypergeometric type IIA assumption.

Table 2 gives the moment estimates of $nj(=10j)$ and $n(n-1)k$ $(=90k)$.

C. hebes is seen to be present in the sward not only in a very large proportion but also very patchily. The other species are all seen to be present in much smaller quantities and more homogeneously. However, *Viola betonicifolia*, for example, forms a greater proportion of the sward than *Rumex acetosella* but shows a lesser degree of clumping.

The numbers of locations and pin observations required for differing numbers of pins per frame, to give the same precision as 200 throws of a frame of 10 pins, have been calculated from the data for each of the five species and are given in Table 3. The numbers of individual pins needed are somewhat higher than those found from Goodall's experimentation but the results are in general agreement.

VII. ACKNOWLEDGMENTS

Grateful acknowledgment is made to Professor D. W. Goodall for permission to use his data and for his helpful advice, and to Dr. William Davies for his continued interest and encouragement.

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APPENDIX I

Estimation of Parameters : Method of Moments

For the distribution

$$P(r) = \binom{-l}{r}\binom{-m}{n-r}\Big/\binom{-l-m}{n},^{*}$$

it is easy to show that

$$\mu_1{}' = \frac{ln}{l+m}, \qquad \ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

$$\mu_2 = \mu_1{}'\frac{(l+m+n)}{(l+m+1)}\frac{m}{(l+m)}. \qquad \ldots\ldots\ldots\ldots \quad (2)$$

Let M and V be the observed mean and variance; n is the number of pins on the frame.

Equate observed with expected values and solve to obtain the moment estimates:

$$l = \frac{\left(n-M-\frac{V}{M}\right)}{\left(\frac{V}{M}+\frac{M}{n}-1\right)}\frac{M}{n}, \qquad \ldots\ldots\ldots\ldots\ldots \quad (3)$$

$$m = \frac{\left(n-M-\frac{V}{M}\right)}{\left(\frac{V}{M}+\frac{M}{n}-1\right)}\left(1-\frac{M}{n}\right). \qquad \ldots\ldots\ldots\ldots \quad (4)$$

Also

$$nj = M, \qquad \ldots\ldots\ldots\ldots\ldots\ldots \quad (5)$$

$$n(n-1)k = V - M\frac{(n-M)}{n}. \qquad \ldots\ldots\ldots\ldots\ldots \quad (6)$$

Estimation of Parameters : Method of Maximum Likelihood

The notation and method used closely follow that given by Bliss and Fisher (1953) for the negative binomial.

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* Adopting the extended factorial notation we define for a and b real

$$\binom{a}{b} = \frac{a!}{b!(a-b)!},$$

where

$$x! = \Gamma(x+1) = \int_0^\infty e^{-t}\,t^x\,dt.$$

and

$$\frac{(-x)!}{(-x-y)!} = \frac{(-1)^y(x+y-1)!}{(x-1)!}, \text{ where } x \text{ and } y \text{ are integers.}$$

Let a_r be the number of locations at which r of the n pins are observed to be in contact with the given species. Then let

$$A_r = a_{r+1}+a_{r+2}+\ .\ .\ .\ +a_n\ ,$$

$$B_r = a_0+a_1+\ .\ .\ .\ +a_{n-r-1}\ .$$

Note that the total number of locations $= A_{-1} = B_{-1}$.

The maximum likelihood equations are derived in the usual way and, using this notation, become

$$0 = F \equiv \sum_{r=0}^{n-1} \frac{A_r}{(l+r)} - A_{-1} \sum_{r=0}^{n-1} \frac{1}{(l+m+r)}, \qquad \ldots\ldots\ldots \quad (7)$$

$$0 = G \equiv \sum_{r=0}^{n-1} \frac{B_r}{(m+r)} - A_{-1} \sum_{r=0}^{n-1} \frac{1}{(l+m+r)}\ . \qquad \ldots\ldots \quad (8)$$

These do not have explicit solutions for l and m hence iteration is necessary. Given initial estimates l_1 and m_1 corresponding values F_1 and G_1 are calculated. Then better estimates l_2 and m_2 may be obtained by solving the following equations:

$$F_1 = (l_2-l_1) \sum_{r=0}^{n-1} \frac{A_r}{(l_1+r)^2} - (l_2-l_1+m_2-m_1)A_{-1} \sum_{r=0}^{n-1} \frac{1}{(l_1+m_1+r)^2}, \qquad \ldots\ldots \quad (9)$$

$$G_1 = (m_2-m_1) \sum_{r=0}^{n-1} \frac{B_r}{(m_1+r)^2} - (l_2-l_1+m_2-m_1)A_{-1} \sum_{r=0}^{n-1} \frac{1}{(l_1+m_1+r)^2}\ . \qquad \ldots\ldots (10)$$

In the five illustrations given, using the moment estimates as l_1 and m_1, on average about five cycles of iteration were needed to stabilize the estimates of l and m to three decimal places.

Calculation of the Expected Frequencies

When estimates of l and m have been obtained, the expected frequencies f_r may be calculated as follows

$$f_0 = A_{-1} \prod_{r=0}^{n-1} \frac{m+r}{l+m+r}, \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (11)$$

$$f_r = \frac{(n+1-r)}{r} \frac{(l-1+r)}{(n+m-r)} f_{r-1}\ . \qquad \ldots\ldots\ldots\ldots\ldots \quad (12)$$

$\sum_{r=0}^{n} f_r$ may be compared with A_{-1} as a check on these calculations.

CONTRIBUTIONS TO AUSTRALIAN BRYOLOGY

I. THE STRUCTURE, DEVELOPMENT, AND SYSTEMATIC AFFINITIES OF MONOCARPUS SPHAEROCARPUS GEN. ET SP. NOV. (MARCHANTIALES)

By D. J. Carr*

[*Manuscript received December 5, 1955*]

Summary

A new thallose hepatic with characters intermediate between those of the Sphaerocarpineae (sensu Müller) and the section Caudiciformes of the Marchantiineae has been discovered on saltpans in north-western Victoria. The female thallus bears a single spherical involucre which has air chambers and specialized pores and contains a single sporophyte. The male plants have not been found. Details are given of the structure and mode of development of the involucre, air chambers, and pores, the early embryogeny of the sporophyte, spore germination, and the development of the thallus. The systematic position of the new plant (*Monocarpus sphaerocarpus*) is discussed and the literature on the relationship between the Sphaerocarpineae and other thallose hepatics is reviewed. The characters of *Monocarpus* are shown to support the view that *Sphaerocarpus* and allied genera should be placed within the Marchantiales rather than with the Jungermanniales. It is proposed to raise a new suborder of the Marchantiales, Monocarpineae, for the single genus, *Monocarpus*. Certain problems of morphogenesis are raised and it is suggested that the enclosure of more than one archegonium in an involucre is conducive to the inhibition of development of more than one sporophyte within the involucre. It is also suggested that growth substances released during meiosis in the sporangium control the post-fertilization growth of the thallus and involucre.

I. Introduction and Description

During the course of an excursion to the Kulkyne National Forest, north-western Victoria, held in conjunction with the recent conference of the Australian and New Zealand Association for the Advancement of Science in Melbourne (August 1955) my wife (née S. G. M. Fawcett) found a new species of liverwort growing on the bare mud of a saltpan by the side of the Calder Highway at Yatpool, adjacent to Red Cliffs. Characteristic higher plants of the saltpan are *Arthrocnemon halocnemoides* Nees and *Salicornia australis* Sol. The habitat is saline although the surface layers of the soil are no doubt considerably leached by the winter rains. The plants, which were very numerous, gregarious, and individually less than 2 mm in diameter, were pale green and had the appearance on the ground of the apical portions of a small *Fossombronia*. Cursory examination showed that the larger thalli, at least, contained an enlarged capsule, and Mr. J. H. Willis, of the National Herbarium, Melbourne, made an inspired guess that the plant might be a *Sphaerocarpus* although no species of that genus are known for Australia and the external appearance of the

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* Botany Department, University of Melbourne.

plant is quite unlike that of *Sphaerocarpus*. Mr. Willis later discovered large populations of the new liverwort on the saltpans at Nowingi further south on the Calder Highway.

The results of a detailed examination of the material collected at Yatpool are given in the present paper. It will be clear that there are many features of the structure and development of this interesting plant which could not be elucidated from the material collected in the field, and it is hoped to establish laboratory cultures from which further data may be obtained. What is so far available is sufficient for at least a partial diagnosis of its characters and for a discussion of its affinities with other thallose hepatics.

Monocarpus sphaerocarpus D. J. Carr; gen. et sp. nov. *Plantulae* annuae, terrestres, dilute virides, ad 2 mm latae, dioecae. Plantae masculae ignotae.

Thallus lobatus membranaceus involucrum involvens maturitate marcescens. Costa nulla. Cellulae grandae ad 140 μ longae. Rhizoides paucae simplices ex basi thalli orientes. *Involucrum* unicum pedicellatum carnosum subglobosum ad 1·5 mm latum. Ad apicem juvenile apertum, ad maturitatem in toto coalescum. Cellulae bullatae. Involucrum cavernosum, porae per parte superiorem aeque dispositae. Pedicellus fuscus, cellulae prosenchymatae. *Archegonia* 3 (rarissime 2) sessilia. *Sporangium* unicum subglobosum, caule brevi, ad maturitatem moro simile ob cellulas rubras integumenti et sporae interiores fuscas. *Sporae* atrae praeter ad maturitatem quaternatim dispositae, 41·5 ± 5 μ diametro latissimo (tuberculis inclusis) facies exterior tuberculata. Tubercula 3·2 μ longa. Sporae involucro et sporangio marcescentibus liberatae.
Type specimen.—National Herbarium, Melbourne.

Portions of the original material will be distributed to the following herbaria:

Royal Botanic Gardens, Kew
British Museum (Natural History), South Kensington
The Museum, Manchester University
Farlow Herbarium, Harvard University, Cambridge, Mass.
Museum national d'Histoire naturelle, Section botanique, Paris
Botanische Staatsanstalten, München
Botanical Museum, University, Uppsala
Botany Department, University College of North Wales, Bangor
New South Wales National Herbarium, Sydney.

A further distribution will be made as more material becomes available.

II. External Appearance of the Mature Plant

The mature plants (Fig. 1) are more or less oblately spheroidal and range in diameter from 0·5 to 2 mm. The thallus is a single-lobed cup-like structure firmly attached by rhizoids to the soil, closely surrounding but not entirely enclosing the single, fleshy involucre, which may be readily detached from it. The rhizoids, which are colourless, simple, and not very numerous, are produced only from the underside of the base of the thallus. The basal part of the thallus is somewhat fleshy where it supports the stalk of the involucre, but the distal, lobed parts are usually one cell thick. The cells of the thallus are polygonal and thin-walled and, like those of other parts of the plant, contain numerous small chloroplasts but no oil bodies. There is no evidence of scales or of mucilage hairs on the mature thallus. It has not been possible to distinguish apical cells in the mature thallus, although an apical cell is present in the sporeling. The top of the sub-spherical involucre is not covered by the lobes of the thallus and under the dissecting microscope its cells appear bullate. Distinct pores, each lying in a slight depression in the surface, are seen to be distributed in a non-random pattern on the upper hemisphere of the involucre (Fig. 2). The mouth of the involucre is quite closed in the mature plant, although its former position is indicated by a slight depression in the surface. A characteristic feature of both mature and somewhat immature plants is the well-organized stalk of the involucre which consists of dark brown, prosenchymatous cells (Fig. 2; Plate 2, Fig. 1), which contrast sharply with the pale green of the thallus and involucre. A single sporophyte is enclosed within the involucre. Of several hundred plants examined only three have been found in which two sporophytes were thus enclosed and these sporophytes were much smaller than the normal.

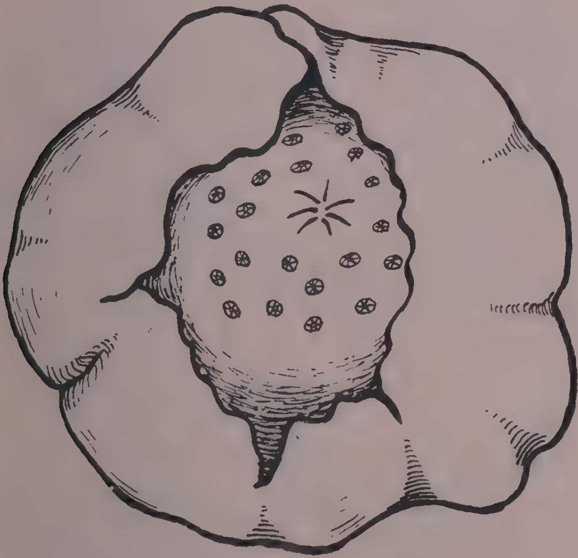

Fig. 1.—Vertical view of mature plant. × 40.

Plants gathered at Yatpool and kept for 3 weeks in the laboratory rapidly matured and decayed. The ripe, dark spores were then easily released from the fragile remains of the involucre and capsule. Despite examination of a large number of thalli ranging from the very smallest (0·1 mm) to the very largest no male plants have yet been found.

III. The Development of the Involucre

Sections of very small plants have shown that the initiation of the involucres takes place very soon in the development of the thallus, when the latter is about 100 μ in diameter. The involucre arises from the thicker basal part of the thallus, the lobes of which continue to develop around the enlarging involucre. The smallest involucres examined consist of the stalk (Plate 1, Fig. 1; Plate 2, Fig. 2) and an expanded platform with a fleshy rim. Three archegonia (rarely two—in very small plants) arise very close together on the centre of the platform. Growth of the involucre takes place at the rim which rapidly forms a cup closely investing the archegonia (Plate 3). At the same time schizogenous air spaces appear within the fleshy tissues of the rim of the cup (Plate 1, Fig. 4; Plate 3). The cells lining these air chambers are densely cytoplasmic and proliferate rapidly giving rise to a small-celled chlorophyllose tissue which lines the air chambers (Fig. 3). Transverse sections of the involucre at this stage in development (Plate 3) show that the air

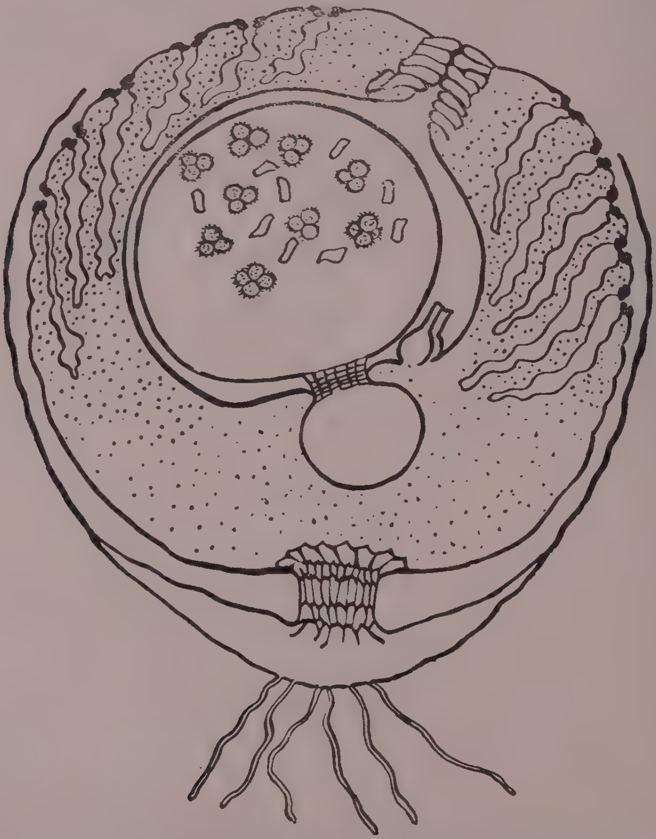

Fig. 2.—Semi-diagrammatic median section of whole plant showing details of involucre and sporophyte.

chambers are fairly regularly distributed and just behind the rim are six to eight in number. Each chamber communicates through a special pore (Plate 1, Fig. 4; Plate 2, Fig. 5) with the air external to the involucre, but there is no connexion with the space within the involucre. The involucre is at first not closely appressed to the sporophyte and its initial growth is much more rapid than that of the capsule. Later the capsule enlarges at a greater rate than the involucre so that at maturity it almost completely fills the space within the involucre (Fig. 2; Plate 2, Fig. 1). Before the capsule is fully formed the mouth of the involucre closes, first forming an irregular pore, then sealing off completely. The growth of the involucre appears to be affected by the proximity of the capsule, that part which is nearest to the capsule growing most rapidly. This unequal growth often causes the suture which represents the closure of the involucre to form on the side from which the capsule is turned away (Plate 2, Fig. 1). As the involucre enlarges more air spaces appear within the tissues particularly of the distal parts and the number of pores on the surface increases. Air spaces also appear within the tissue partitions which formerly separated the first-formed air chambers so that the number of chambers increases with increasing diameter of the cross section. The air chambers remain separated by walls of chlorophyllose cells.

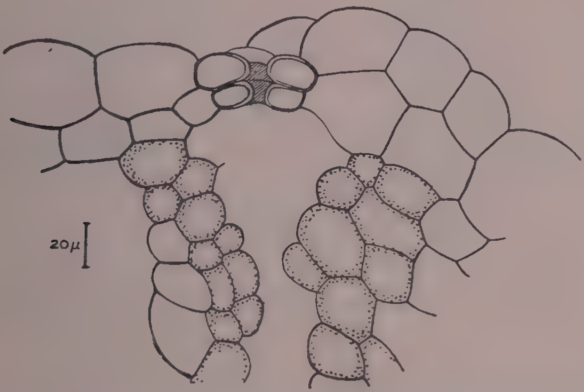

Fig. 3.—Part of involucre showing L.S. through pore and air chamber.

IV. The Pores

The pores have a well-defined structure and are reminiscent of those of the Marchantiineae. Each pore arises from a single epidermal cell overlying a schizogenous air space which separates it from the hypodermis (Fig. 4). The pore initial remains small while the surrounding epidermal cells become enlarged and bullate. Thus the pore initial becomes depressed below the level of the surrounding epidermis. The sequence of divisions has not been fully elucidated but it appears that the pore initial divides periclinally and each of the two superposed cells then divide twice anticlinally (Fig. 5). The four epidermal cells may each divide again by a radial anticlinal wall so that a cell arrangement resembling a cake cut into eight segments is developed. Occasionally one, two, or three of the cells will fail to carry out the final division so that the cake consists of from 5 to 8 segments, but 8 and 6 are the most frequent numbers. The four hypodermal cells do not divide again. At the same time as these divisions are in progress the cells separate at their intersections over the future pore. The inner pore is roughly square or rectangular (from separation of the intersection of the four hypodermal cells) but the outer pore, which is much the larger, is generally octagonal or hexagonal. The cell walls bounding the pore are thicker than those distal to the pore (Fig. 3; Plate 2, Fig. 5). The pores are numerous and regularly spaced on the upper half of the mature involucre and usually absent from or rare on the lower half (Fig. 6).

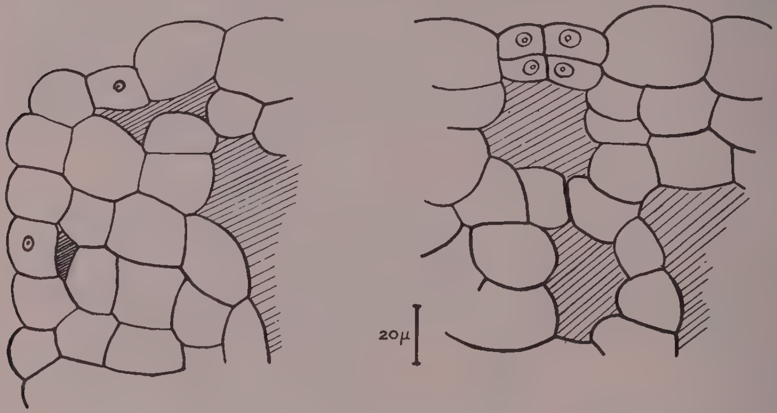

Fig. 4.—Part of the rim of a developing involucre (L.S.) showing origin of air chambers (shaded areas) and pore initials (cells with nuclei shown). (Camera lucida drawing.)

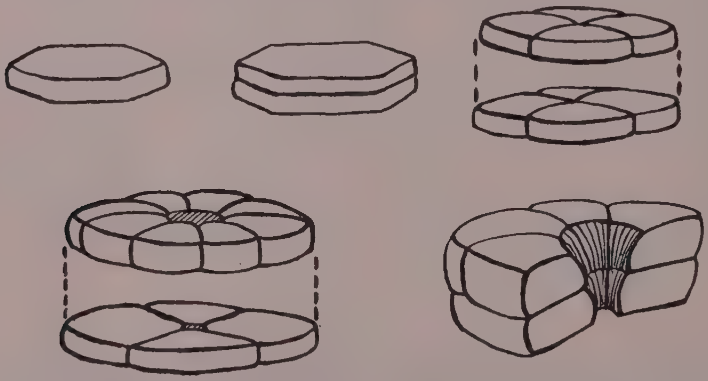

Fig. 5.—Diagram to illustrate divisions of pore initial and development and structure of pore.

The air chambers enlarge downward by schizogeny into the fleshy tissues of the involucre. The cessation of enlargement of the pore initial may be accompanied by a cessation of enlargement of cells immediately below the future pore. Thus schizogeny may take place along lines of weakness (where growth is reduced) within the enlarging involucre. Since the cells tend to be arranged in regular rows extending inwards from the surface the splitting-apart of files of cells may be facilitated. However, as soon as the pore is established the cells lining the air chamber proliferate to form a tissue of small cells, the walls of which bulge into the cavity (Fig. 3).

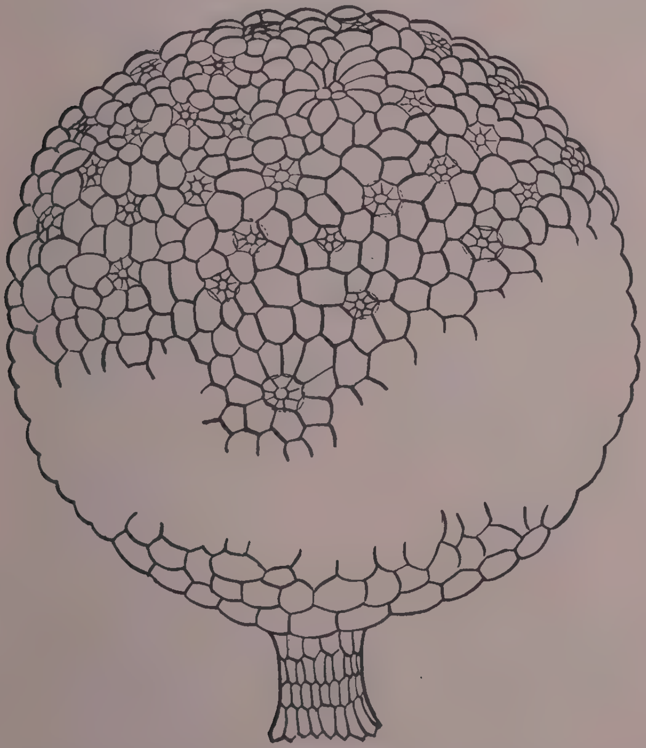

Fig. 6.—Semi-diagrammatic view of detached involucre showing details of stalk, pore distribution, and closure of mouth.

V. The Closure of the Involucre

The cells of the suture which marks the closure of the involucre have a characteristic structure (Plate 2, Fig. 1). They are clavate, their enlarged ends abutting to form a thickened tissue quite unlike that of the rest of the involucre. There are no air chambers or pores in this tissue, which completely closes the mouth. It is clear that the early growth of the involucre takes place by cell division and enlargement at the rim. It might also be thought that these clavate cells constitute a meristem contributing to the further enlargement of the involucre but since the closure of the involucre takes place while the capsule is still quite small growth must take place subsequently over the whole surface. If cell division and cell enlargement were restricted to the cells surrounding the mouth, the mature involucre would be obpyriform (as it is in some species of *Sphaerocarpus*) but in fact the involucre remains more or less spherical from the time of closure until full maturity.

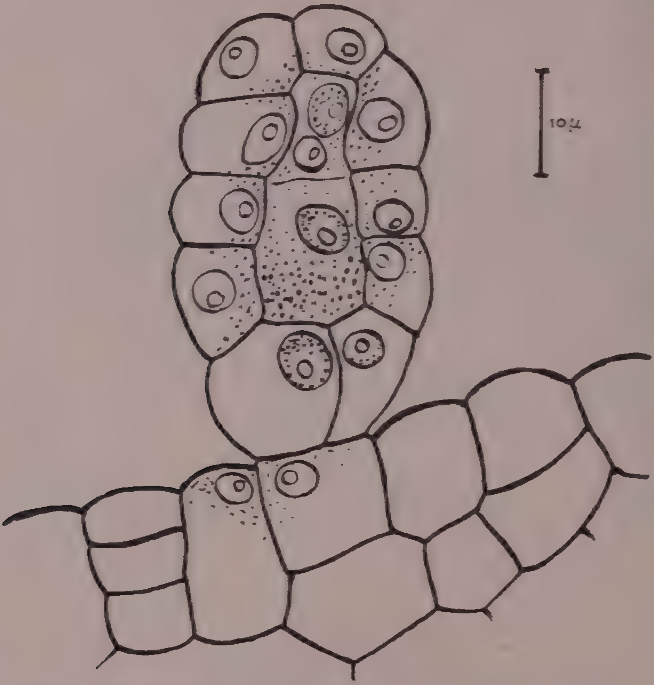

Fig. 7.—Early stage in development of archegonium (reconstructed from serial sections). (Camera lucida drawing.)

VI. The Archegonia

The early development of the archegonium appears to be similar to that of other Marchantiales (Fig. 7). Even on thalli as small as 200 µ in diameter the archegonia may be fully mature. The venter is initially one cell thick except at its junction with the platform of the involucre. The cells of the venter, whether fertile or not, later divide periclinally so that the wall becomes two cells thick. The neck consists of 6 rows of cells (Plate 3, Fig. 2) and the terminal cells are not divaricate when mature. Of the three archegonia usually only one gives rise to a sporophyte. The venters of each of the other two enlarge considerably and in each the ovum degenerates into an amorphous body which stains deeply with haematoxylin (Plate 1, Fig. 4). The two infertile archegonia are usually thrust aside by the expansion of the platform of the involucre around the foot of the developing sporophyte and they have frequently been observed in a lateral position on the inner wall of the involucre. They are conspicuous in dissected plants by their very swollen and apparently empty venters and the brownish colouration of the neck cells.

VII. The Sporophyte

The initial development of the sporophyte is shown diagrammatically in Figure 8. An early stage is shown in Plate 1, Figure 3. There are three nuclei in the venter and the cell plate segregating the lowermost has already formed. The cytoplasm associated with the hypobasal nucleus is more vacuolate than that in the upper part of the venter. The first wall of the embryo is thus clearly transverse, as it is in the Sphaerocarpineae and in the section Caudiciformes of the Marchantiineae.

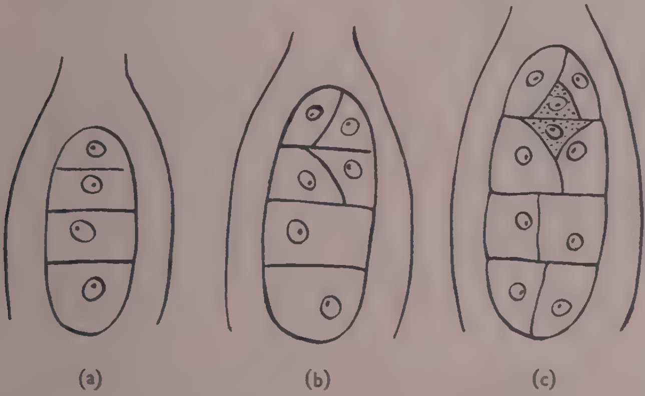

Fig. 8.—Diagram to illustrate early embryogeny of sporophyte. Stippling represents differentiation of endothecium from exothecium.

In Plate 2, Figure 2, a later stage in the development of the embryo is shown. The embryo consists of four superposed cells of which the two lowermost are divided in the plane of the section (see Fig. 8(*c*)). The hypobasal cell thus divides at an early stage in embryogeny, unlike that of *Geothallus* (according to Campbell (1896)). Presumably the two basal cells give rise to the foot and seta respectively. The two upper cells divide by oblique walls, initiating the differentiation of the sporogenous cells from the capsule wall cells. In the older embryo shown in Plate 1, Figure 4, the sporogenous tissue is already well developed. (The foot is turned away from the plane of the section and is only vaguely indicated in the photograph.)

The foot of the mature capsule is more or less spherical and its cells stain densely (Plate 2, Figs. 1 and 3). The seta is short, consisting of 5 or 6 outer tiers each of 5 or 6 short cells surrounding a central row of 4 cells (Plate 2, Fig. 3). The cells of the seta are brown like those of the involucral stalk. The wall of the capsule consists of a single layer of very thin cells fairly regularly hexagonal in outline. The capsule is only loosely filled by sporogenous tissue—a feature noted also by Campbell (1918) in *Sphaerocarpus* and *Geothallus*. Some tetrad formation occurs at a very early stage in the development of the capsule. Meiosis is not simultaneous throughout the sporogenous cells and at any stage in the development of the sporophyte numbers of "sterile cells"—which are probably presumptive spore mother cells—can be distinguished among the spore tetrads (Plate 2, Fig. 3). The progressive differentiation of the sporogenous tissue is undoubtedly responsible for the great range in size to be found among mature capsules. Presumably growth of the capsule, involucre, and thallus continues as long as meiosis continues in the sporogenous tissue, and the number of mature spores may be either very small—possibly as low as 80—or very large. As soon as the plants are subjected to drought the spores which have been formed mature and separate from the tetrads and further meiosis ceases. Thus the number of "sterile cells" is always greater in sporophytes dissected at an early stage in development and they may be entirely absent from very large capsules. On the other hand the number of spores increases with increasing size of the capsule. The so-called "sterile cells" are thus very probably sporogenous cells the meiosis of which has been delayed.

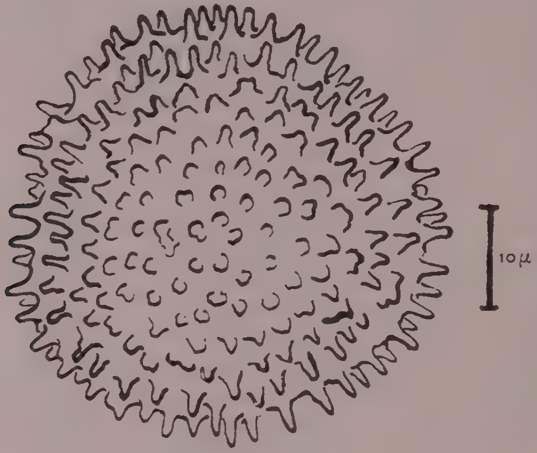

Fig. 9.—Spore.

VIII. The Spores

The mature spores are very dark and tuberculate or even almost spinose on the outer face (Fig. 9; Plate 2, Fig. 4). Just before maturity, when the spores are still in tetrads, they are yellow. The dark colour appears only on complete maturity, when the spores separate from the tetrads. In section (Plate 2, Fig. 3) the spore wall is seen to consist of two membranes, an inner, smooth and coloured one, about 1 μ thick, and an outer one which is almost hyaline and is prolonged into the tubercles. The spores appear to be vacuolate and are uninucleate.

IX. The Sporeling

In view of the very precocious formation of the reproductive structures it will be essential to be able to germinate the spores and grow the plants on a nutrient medium in order to elucidate further the initiation and development of the involucre and archegonia, and to detect the male plants. The preparation of serial sections from the original material has been rendered difficult by the adhering soil particles. Of a very large number of spores sown on 1·5 per cent. agar with Benecke's solution (Müller 1954, p. 164) only a few have germinated after 2 months. The mode of germination is similar to that described for *Sphaerocarpus* and *Geothallus*. A short "protonemal filament" is developed (Fig. 10) and this usually becomes "angled" by the production of an apical cell in a lateral position. The apical cell gives rise to a flat plate initially 2-3 cells wide. Older thalli are heart-shaped with a two-sided apical cell lying at the base of the notch. The cells are inflated and dark green in colour. Rhizoids are produced from the underside. Dorsiventrality is apparently light-induced since on agar in inverted petri dishes the dorsal, non-rhizoidal surface was found to be that appressed to the agar, i.e. proximal to the light source. A peculiar feature is the production of stalked glands or papillae from marginal cells of the thallus (as in the prothalli of *Sphaerocarpus* and of many Polypodiaceous ferns). The distribution of these glands is very uniform, and every fourth or fifth cell derived from the apical cell produces a gland.

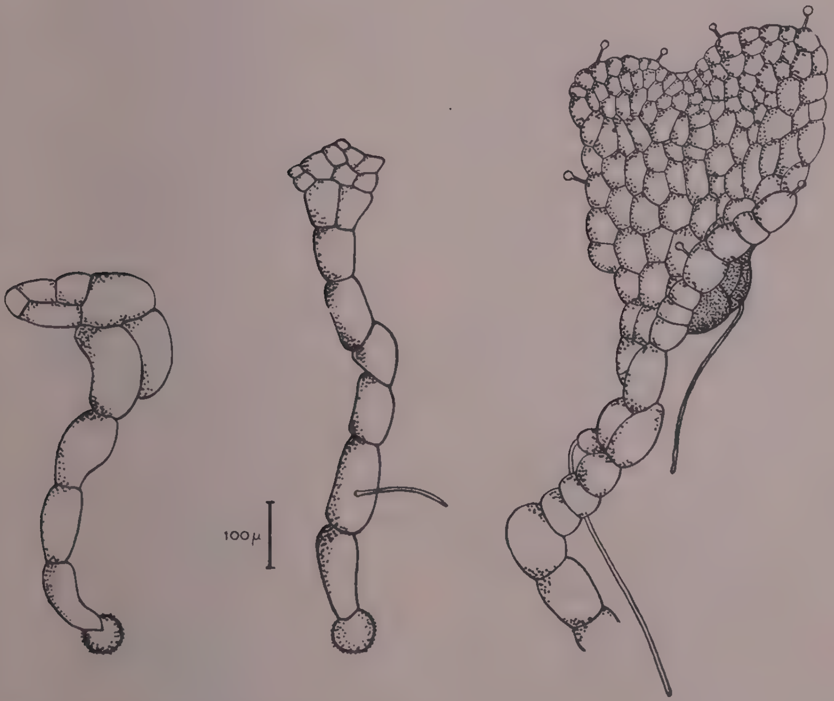

Fig. 10.—Three stages in the development of the sporeling. (Camera lucida drawings.)

X. Discussion

(*a*) *Affinities of* Monocarpus

The affinities and systematic position of *Monocarpus* pose questions of considerable interest. The plant has characters which suggest a relationship with *Sphaerocarpus.* The large involucre is borne on an insignificant thallus which is more than one cell thick only in the central portion and has no air chambers or specialized pores or ventral scales. The smooth-walled rhizoids, absence of oil bodies and elaters, and dissolution of the sporangium wall at maturity are characters common to both *Monocarpus* and *Sphaerocarpus*, and the mode of germination and the sporelings are similar in both genera. On the other hand the presence of air chambers and specialized pores in the involucre are characters which transgress the boundaries of the suborder Sphaerocarpineae (Müller 1954) and indicate affinities with the suborder Marchantiineae of the Marchantiales. *Monocarpus* differs from *Sphaerocarpus*, *Geothallus*, and *Riella* in that the archegonia are few in number (3 or rarely 2) and are enclosed in a single involucre, whereas in those three genera each of the numerous archegonia is enclosed in its own involucre.* In all four genera the single layer of jacket cells in the capsule and the six-tiered archegonial neck mitigate against their inclusion in the Jungermanniales.

The systematic position of *Sphaerocarpus* has been considerably disputed during the last 100 years. Gottsche, Lindenberg, and Nees (1844) placed it in their Tribe Ricciae. Leitgeb (cited by Schiffner 1909) was followed by Wettstein (1901) in placing *Sphaerocarpus* and *Riella* together in the anacrogynous Jungermanniales, and this viewpoint has been accepted by Frye and Clark (1937). Goebel and Lotsy on the other hand saw greater resemblances to the Marchantiales (see Goebel 1915-17), while Cavers (1910) combined the two genera into a separate order, Sphaerocarpales, which he placed near to, but independent of the Marchantiales. This affinity to the Marchantiales is also stressed by Buch, Evans, and Verdoorn (1937). Müller (1954) has recently discussed the systematic position of *Sphaerocarpus.* He quotes unpublished work of Lorbeer (recently confirmed by Yuasa (1954)) according to which both Sphaerocarpineae and Marchantiineae "have similarities in the discharge of the antheridia and differ in this process from the other hepatics, and the spermatozoid is identical in both groups (attachment of the two flagella at the tip)". In the Jungermanniales the flagella are inserted one behind the other. Apart from this new evidence, Müller points out the similarities between the storied early embryos of *Sphaerocarpus* and those of the members of the section Caudiciformes (*Targionia* etc) of the Marchantiales. Among other features the absence of elaters and the cleistocarpic dehiscence of the sporogonium and its single cell layer are clearly at variance with an alliance between *Sphaerocarpus* and the Jungermanniales. Müller therefore agrees with Goebel and Lotsy on the matter and includes *Sphaerocarpus*, *Riella*, and *Geothallus* in a suborder of the Marchantiales, the Sphaerocarpineae, with two families, Sphaerocarpaceae and Riellaceae. Since, as stated above, certain characters of *Monocarpus* (air chambers, pores, number of archegonia per involucre) transgress the boundaries of the suborder Sphaerocarpineae it seems advisable to raise a new suborder for it, Monocarpineae. The affinities of this suborder would be with the Sphaerocarpineae on the one hand and with the section Caudiciformes of Marchantiineae on the other. It may be placed in Müller's system (1954, p. 195) as "Suborder AA, Monocarpineae; Family 4 A, Monocarpaceae; *Monocarpus*".

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* Two archegonia have occasionally been found within one involucre in plants of *Sphaerocarpus* (see Proskauer 1954).

(*b*) *Problems of Morphogenesis*

From the point of view of differentiation and development *Monocarpus* presents some interesting problems. The origin of air chambers in the thallose hepatics has been the subject of considerable controversy. Goebel adhered to the views of Leitgeb (1880) on the matter (see Goebel 1915-17, Heft II, p. 614). Following the work of Barnes and Land (1907), Deutsch (1912), and O'Keefe (1915), it is generally accepted that the air chambers arise in the Marchantiales from an initial and progressive schizogeny in the hypodermal or epidermal cell layers. In the involucre of *Monocarpus* the air chamber arises by internal schizogeny below an epidermal cell which remains small and is depressed below the general epidermal surface. The pores of the Marchantiineae are bounded by cells cut off from the cells at whose junction the initial epidermal schizogeny occurs. Although the external appearance of the pores in the involucre of *Monocarpus* resembles that of the pores of the Cleveaceae, they differ both in structure and mode of development from the pores of any of the Marchantiineae. They originate from a single pore initial which undergoes periclinal and anticlinal divisions, the pore finally appearing by separation of the derivative cells at their line of junction. Also the pores are bounded by *two* layers of cells.

The regularity of distribution of the pores on the upper half of the involucre recalls the similar regular distribution of pores in species of Marchantiineae. While the involucre is growing at its apical rim new air chambers and pores appear serially and acropetally in the newly formed tissues. It is possible that the regular distribution of the pores is attributable to a regular pattern of differentiation among the immediate derivatives of the "rim meristem". The regular distribution of idioblasts and stomata in the epidermis of leaves of grasses is an example of pattern controlled by the sequence of cell divisions (see Bünning 1953). On the other hand the number of pores (and of air chambers) increases with increasing size of the involucre, and it is probable that new pores are initiated between the original ones. Thus the spacing of the pores shown in Plate 3, Figure 1 is much greater than the spacing shown in Figure 11 (taken from a large mature plant). The regularity of distribution suggests that the sites where the new pores can arise must lie outside the "morphogenetic field" of adjacent pores. If each pore is considered to exert an influence suppressing the potentiality of pore formation in a "field" around itself, then the new pores arise where, as a result of growth and cell division, a gap appears between the fields of adjacent pores. Thus the distance or epidermal cell number between pores is kept more or less uniform.

The absence of pores or air chambers in the tissue formed at the closure of the involucre suggests that the cells of this tissue have properties that are quite different from those of the rest of the involucre. This is also apparent in the difference in size and shape—they are much larger than the other involucral cells and are clavate. The absence of pores in this "closure tissue" may be compared with the absence of stomata in certain parts of the epidermis (e.g. over the veins) of higher plants, which overlie specialized structures.

The early initiation of the archegonia recalls the observations of Leitgeb (cited by Goebel, loc. cit., p. 557) in which he found "sex organs initiated on germlings (of *Sphaerocarpus*) with an average diameter of 0·1 mm". In *Monocarpus* also, archegonia may be initiated on germlings almost as small. The enclosure of two or three archegonia within a single involucre would seem to permit the development of as many sporophytes, but in fact it is only very rarely that even two of these develop within one involucre. This is a common phenomenon in the Hepaticae and it has been remarked by many authors. To quote Goebel (1915-17, English Edition, p. 83) "usually only a single embryo develops into a sporangium and this bores into the tissue underneath the archegonium; in *Pellia calycina* I have occasionally found two sporangia within one envelope but they were unequally developed". In *Monocarpus* the egg-cells of the infertile archegonia undergo some hyperplastic change as soon as an embryo begins to develop in the fertile archegonium. There appears to be some sort of correlative inhibition exerted by the developing embryo on the egg-cells of the other archegonia. This inhibitory influence may be of the same nature as that which Bünning (1953) suggests is responsible for the inhibition of development of the remaining ovules by a developing embryo in the fruit of *Quercus* (see Bünning 1953, p. 248). If this is the case, then the enclosure of the archegonia in separate involucres in the Sphaerocarpineae would appear to prevent the inhibition of the younger zygotes or embryos by the older. It is significant

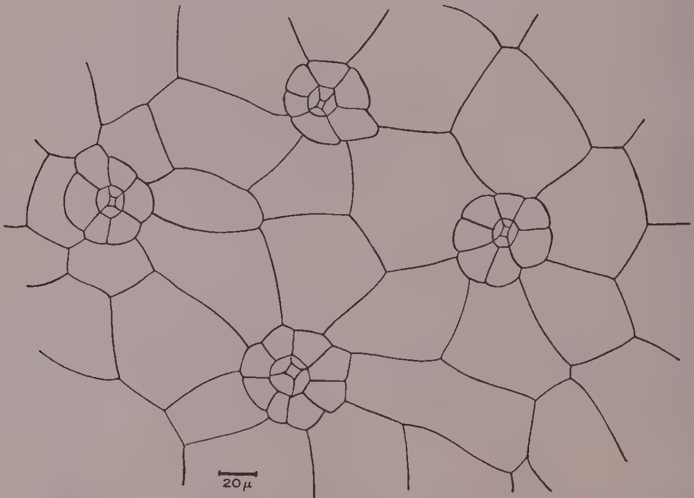

Fig. 11.—Part of surface of mature involucre showing external appearance and regular distribution of pores. (Camera lucida drawing.)

that in these three genera the archegonia are produced serially and acropetally—a mode of development which would have small biological advantage if the earliest formed sporophyte were able to inhibit the development of those situated more acropetally. Thus, either the enclosure of each archegonium in its own involucre may represent a delimitation of the inhibitory field of the young embryo or the involucre itself may constitute a barrier to the spread of the inhibition.

As against these inhibitory effects, the developing sporophyte exerts stimulatory effects on the development of the surrounding vegetative tissue, the involucre, involucral stalk, and thallus lobes. This is clearly shown in the lateral position of the suture of the involucre when the capsule develops laterally. Moreover, the involucre and thallus expand with the expanding sporophyte so that (after the closure of the involucre) the latter remains closely invested. Since the diameter of the sporophyte may increase up to 1 mm the surface area of the thallus and involucre may increase several hundredfold during the period of growth of the sporophyte. The stalk of the involucre also becomes noticeably more robust during this period. The continued growth of the vegetative parts of the plant may be attributed to stimulatory effects exerted from the capsule itself, and it is not impossible that some growth substance is released during the meiosis of the sporogenous cells, as has been suggested to explain the sudden but temporary acceleration of the growth of flowering plants at times corresponding with meiosis (of pollen and megaspore mother cells) and syngamy (Wittwer 1943). Thus the meioses of the sporogenous cells may stand in the same relation to the growth of the rest of the plant as the developing ovules (supplying growth substances) to the growth of an angiospermic fruit. If this is the case then the delayed meiosis which occurs in *Monocarpus* (and possibly also in *Sphaerocarpus*) may result in a gradual and continued production of such a growth substance and consequently enable the plants to continue growing as long as unfavourable conditions such as drought do not intervene. With the onset of drought the plants mature rapidly and die and those spores which have been formed, whether numerous or few are ready to be released.

Although there are cases on record (see Gross and Allen 1938) where sterile cells in *Sphaerocarpus* have been found to have 2 or 4 nuclei (which might indicate that meiotic divisions occur in them) Gross and Allen have shown that the nuclear divisions in the sterile cells of *S. donellii* are mitotic. However, the same diversity in size of sporangium and number of spore tetrads occurs in *Sphaerocarpus* (see Proskauer 1954) as in *Monocarpus*, and the suggestion made above concerning the nature of the sterile cells may help explain this phenomenon.

XI. Acknowledgments

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EXPLANATION OF PLATES 1–3

PLATE 1

Longitudinal sections showing early embryogeny of the sporophyte.

Fig. 1.—Archegonium (fertilized ?) and young involucre. Egg-cell enlarged but undivided. × 220.

Fig. 2.—Storied embryo showing initial differentiation of sporogenous cells (endothecium) from wall cells (exothecium). × 610.

Fig. 3.—Early embryo showing three nuclei and transverse first division. × 450.

Fig. 4.—Late embryo showing well-developed sporogenous tissue. Note the enlarged and degenerate egg-cell of the infertile archegonium. The foot of the embryo lies off the plane of the section. The air chambers of the involucre and a section through a pore (P) are shown. × 220.

PLATE 2

Fig. 1.—Median section of whole plant with young sporophyte. Note the prominent involucral stalk and the closure tissue of the involucre (at *C*). × 115.

Fig. 2.—L.S. young involucre and archegonium. The stalk of the involucre is off the plane of section. × 140.

Fig. 3. L.S. sporophyte. Section shows spores in section and "sterile cells" in capsule. × 200.

Fig. 4.—Spore (optical section at boundary). × 740.

Fig. 5.—External aspect of pore bounded by eight cells. × 410.

PLATE 3

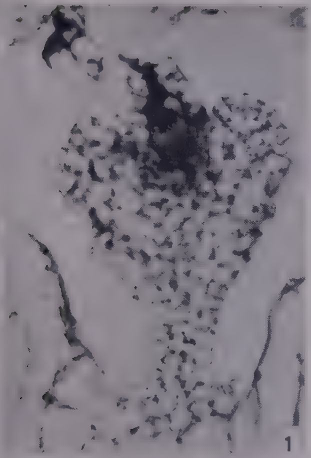
Transverse sections at three descending levels of a young involucre. All × 195.

Fig. 1.—Section of the top of the involucre and tips of necks of two archegonia. Inner cells of pores shown at *P*, other pores located at *PL* (not quite in plane of section).

Fig. 2.—Section through archegonial necks and about half way down the involucre. Note regular distribution of air chambers.

Fig. 3.—Section at level of venters of two of the archegonia. *A*, fertile archegonium; *S*, sterile archegonium.

CONTRIBUTIONS TO AUSTRALIAN BRYOLOGY. I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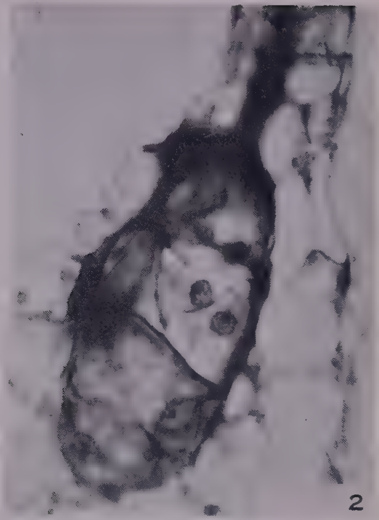
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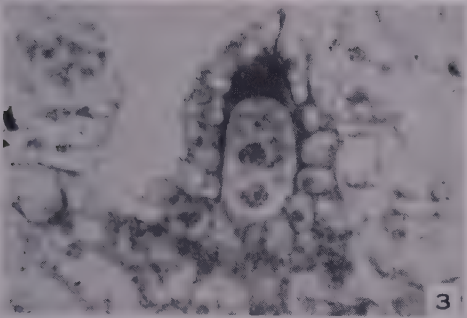
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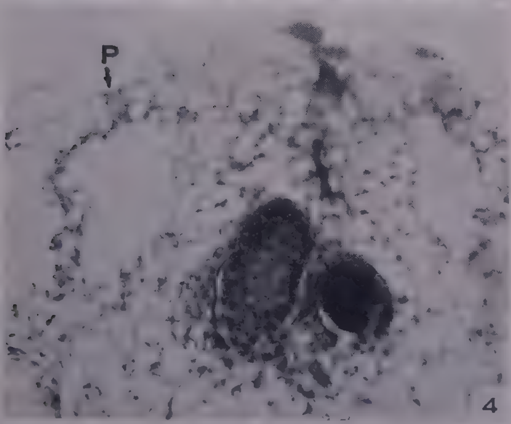

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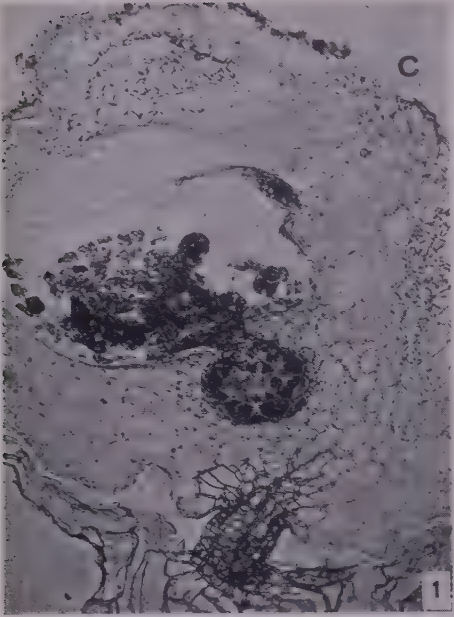

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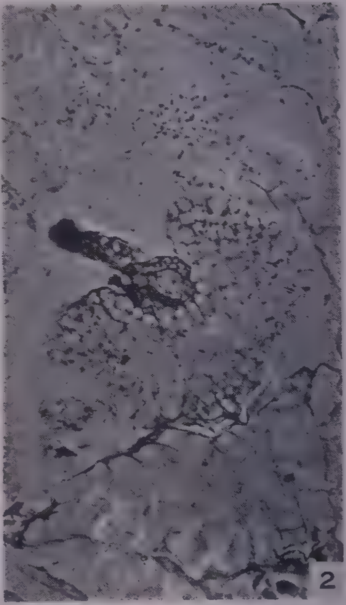
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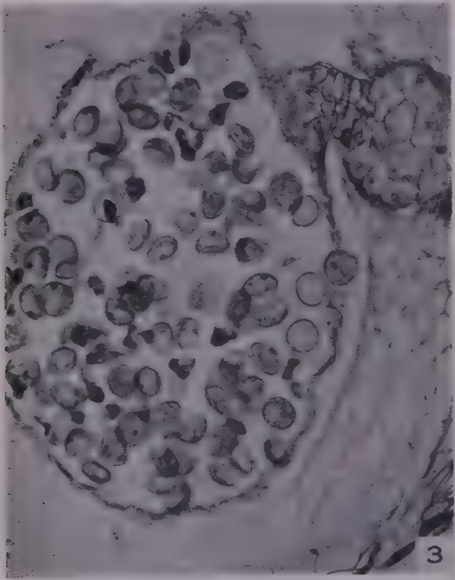
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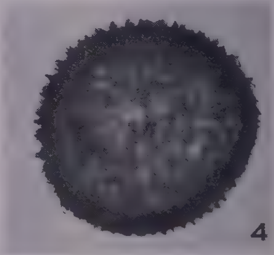
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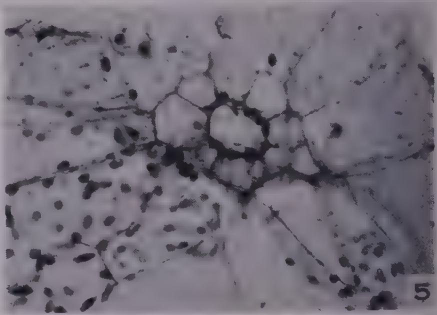
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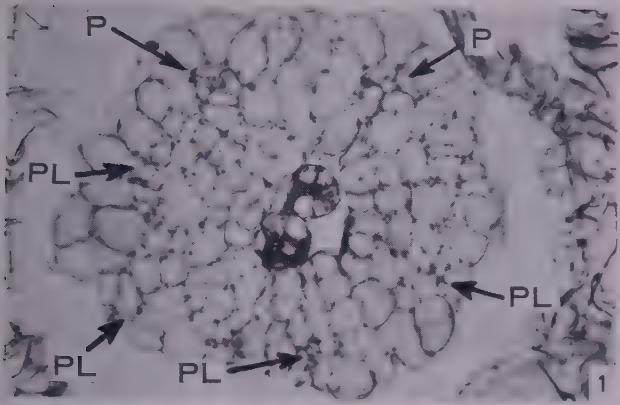
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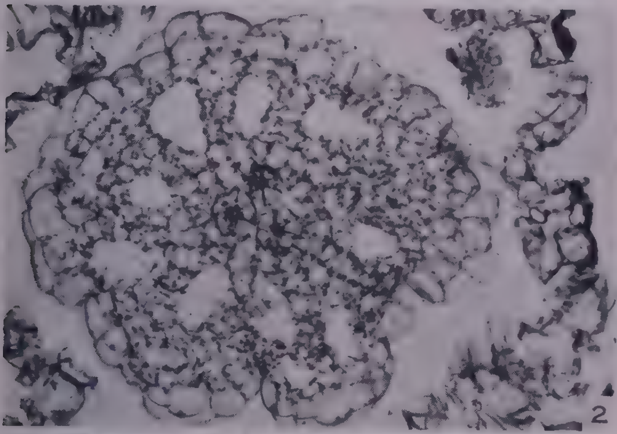
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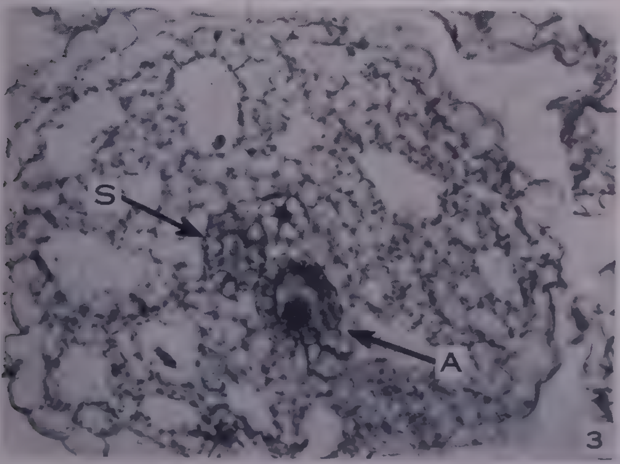
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THE NATURE OF SURFACE GROWTH IN PLANT CELLS

By A. B. Wardrop*

[*Manuscript received July* 19, 1956]

Summary

Autoradiographs have been prepared from parenchyma isolated from *Avena* coleoptile segments grown in a medium containing labelled glucose. The autoradiographs show that there is no concentration of radioactive material at the cell tips and labelled cellulose appears to be uniformly distributed in the cell wall. Electron micrographs of similar material show that the cellulose microfibrils are almost transversely oriented on the inner surface of the cell wall but are considerably dispersed from this direction on the outer surface. From this evidence it is concluded that growth in coleoptile parenchyma is not of the "bipolar" or "mosaic" types previously suggested, but corresponds to the "multi-net growth" of Roelofsen and Houwink. In addition a study has been made of the relation of microfibril orientation to cell form in parenchyma of onion root and in roots after treatment with colchicine, from which it is concluded that the final microfibril orientation on the outer wall surface is determined by the extent and polarity of its surface growth.

I. Introduction

In a previous contribution to this journal (Wardrop 1955), evidence was presented in support of the view that in parenchyma cells of *Avena* coleoptiles growth was not confined to the tips of the cells (Mühlethaler 1950) but was distributed over the cell surface. This conclusion was based on the observation that there was a progressive separation of the pit fields in cells taken from coleoptiles at successive stages of growth. In addition this change was paralleled in the same cells by a progressive dispersion from a transverse orientation of microfibrils on the outer surface of the cells.

In this work it was assumed that new microfibrils were incorporated into the expanding structure of the primary wall in the region of the pit fields and at points of penetration of the wall by plasmodesmata. This view represented a modification of the view of Frey-Wyssling and Stecher (1951) and Stecher (1952) according to which synthesis of microfibrils took place at points over the cell surface where the cell wall was transiently penetrated by the protoplast.

A different concept of surface growth has been presented by Roelofsen and Houwink (1953) and Houwink and Roelofsen (1954) and termed by them "multi-net growth". This was based on the observation that in the case of certain seed hairs and the stellate pith cells of *Juncus* the microfibrils of cellulose are transversely oriented to the major cell axis on the inner surface of the wall, and are considerably dispersed from this orientation on the outer surface. It was concluded that transversely oriented microfibrils are deposited continuously on the inner surface of the cell wall during its extension. These microfibrils adhere loosely to

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each other so that during extension the transversely oriented microfibrils become disoriented like a net. This disorientation will be greatest on the outer surface of the cell because more extension has taken place since they were deposited.

In the parenchyma of *Avena* coleoptiles morphological investigations as to the exact mechanism of surface enlargement is also of physiological importance as it takes place under the control of endogenous auxin. In a more general way surface growth forms a phase in the differentiation of cells generally and its amount and polarity determine the ultimate form the developing cell assumes, so that the mechanism of the process and the factors governing it have considerable morphogenetic implication.

In this paper a further investigation has been made of the nature of surface growth in coleoptile parenchyma for two reasons: firstly, to determine if the multi-net type of growth of Houwink and Roelofsen here applies, as the evidence presented previously (Wardrop 1955) would not be inconsistent with such a concept (because only the outer surface of the cells were examined) and, secondly, to attempt to determine the site or sites of cellulose synthesis, using radioactive tracer techniques. In addition, the investigations have been extended to other tissues in an attempt to relate the cell wall organization to the cell form as a first step to a study of the role of surface growth in cellular differentiation.

II. Experimental and Results

The present study began with the examination of coleoptile parenchyma of oat with a view to determining any difference in microfibril orientation on the inner and outer surfaces of the cell wall as demanded by the concept of multi-net growth. Coleoptiles of the variety Algeribee were grown to a length of 3 cm and the sub-terminal 5 mm was macerated in the manner described previously (Wardrop 1955). After maceration the cells were disintegrated in a mechanical disintegrator mounted on collodion-covered grids and shadow cast with uranium with the metal beam making an angle of approximately 10° with the specimen surface. These preparations were then examined in an R.C.A. type E.M.T. electron microscope. A typical electron micrograph so obtained is shown in Plate 1, Figure 1. The difference of orientation on the inner (I) and outer (O) surfaces of the cells is apparent. Similar results were obtained with the parenchyma of onion root (Plate 1, Fig. 2).

The effect of extension on the progressive disorientation of the microfibrils previously reported (Wardrop 1955) was further investigated under differing conditions affecting the degree of surface growth and cellulose synthesis.

Coleoptiles were grown to a length of 3 cm and the sub-terminal 5 mm were cultured under the conditions shown in Table 1. Electron microscopic examination of parenchyma isolated from segments grown under these conditions showed no noticeable difference except in the case of the 3-indoleacetic acid–sucrose–mannitol medium, where synthesis of cellulose was favoured by the sucrose (Bonner 1934) but growth was restricted by the mannitol.

The third phase of the investigation related to an attempt to determine the regions of cellulosic synthesis in the cell. To this end, it was considered that a suitable approach would be to culture coleoptile segments *in vitro* in the presence of labelled glucose, and to study subsequently, by autoradiography, the distribution of labelled cellulose synthesized from it. Accordingly, 5-mm segments were cut from coleoptiles 3 cm in length, the terminal 3 mm being rejected. These segments were then cultured at 25°C in a glucose solution containing 10 μc of labelled glucose in 5 c.c. the total glucose concentration being adjusted with unlabelled glucose to 1 per cent. In addition, the medium contained 3-indoleacetic acid (IAA) at a concentration of 1 mg/l. The segments extended 48 per cent. in 12 hr. After the period of growth the segments were macerated by alternate treatments with 0·1N sodium hydroxide and 0·1N hydrochloric acid. After thorough washing the suspension was allowed to flow on to glass slides and dried. Autoradiographs were prepared by the stripping film method, using Kodak Scientific Plates, Autoradiographic. The film was developed after 3 months' exposure. Typical autoradiographs so obtained are shown in Plate 2, Figures 1–4.

TABLE 1

THE EXTENSION OF AVENA COLEOPTILE SEGMENTS UNDER DIFFERENT CONDITIONS

Conditions of Culture	Extension (%)
Control (fixed)	—
25°C—1 mg/l IAA	59
25°C—1 mg/l IAA + 1% sucrose	82
4°C—1 mg/l IAA	40
25°C—1 mg/l IAA + 1% sucrose + 0·35M mannitol	51

It is clear that there is no evidence that cellulose deposition was confined to the cell tips. It is less clear whether deposition was completely uniform over the cell surface or confined to the region of the pits. However, as these structures are often grouped, it would seem that the assumption of a completely uniform synthesis of cellulose over the cell surface is most consistent with the evidence presented. In Plate 2, Figure 3, longitudinal bands are visible in the autoradiograph undoubtedly corresponding to bands of secondary thickening of cellulose. This is in accord with the view (Wardrop 1955) that secondary thickening need not impede extension growth.

The cell shown in Plate 3, Figure 2, gives an indication of the way in which the microfibril orientation may be partially altered experimentally. A more extreme modification can be achieved, however, by greatly altering the cell form by treatment with colchicine. For this purpose onion roots were allowed to grow in a 1 per cent. solution of colchicine over a period of several weeks. The resulting change in root form thus achieved was reflected in the form of the parenchyma isolated from regions 2 mm from the root tip which are shown in Plate 4, Figures 1 and 2. Corresponding electron micrographs are shown in Plate 4, Figures 3 and 4.

III. Discussion

From Plate 1, Figures 1 and 2, it is clear that both in the parenchyma of *Avena* coleoptiles and of onion root respectively there exists a difference in orientation of the microfibrils on the inner and outer surfaces of the cell wall. The greater dispersion of the microfibrils on the outer as compared with the inner surface is directly comparable with results already reported for cotton hairs, the hairs of *Asclepias*, and the stellate pith parenchyma of *Juncus* (Roelofsen and Houwink 1953; Houwink and Roelofsen 1954).

Considered dynamically, this result must mean, as Roelofsen and Houwink (1953) have pointed out, on the assumption that the microfibrils are always oriented transversely on the inner surface, that relative movement between microfibrils must take place as growth proceeds. It follows further that the amount of resultant disorientation in the outer surface of the cell wall depends on the amount of extension which had taken place at the stages of growth examined. This would explain the progressive disorientation observed in the investigations previously described for *Avena* (Wardrop 1955). This is confirmed by the observations illustrated in Plate 3, Figure 2, in which it can be seen that, when extension growth of excised segments was limited by the inclusion of a hypertonic solution of mannitol, the disorientation on the outer surface was relatively small in comparison with the segments extended in the absence of mannitol (Plate 3, Fig. 1).

These observations must be taken as consistent with the suggestion of Heyn (1931) that extension growth under the influence of auxin involves an increase in cell wall plasticity, although Heyn did not stipulate whether this change resulted from the direct or from the indirect action of auxin. The specific nature of this mechanism has been indicated in recent studies by Ordin, Cleland, and Bonner (1955), in which it was demonstrated that auxin influences the metabolism of the hot-water-soluble non-cellulosic fraction of the cell wall.

The demonstration of the multi-net type of growth in *Avena* coleoptile parenchyma also gives an explanation of the early observation of Bonner (1935) that the sign of birefringence did not change in the parenchyma as extension growth proceeded. The transverse orientation of the microfibrils on the inner surface of the cell wall must always favour such a result, especially in immature cells, and, so long as the extension is not of such a magnitude that the contribution of the microfibrils in the outer regions of the cell wall does not exceed that of the inner and intermediate zones of the wall statistically, a net transverse orientation as indicated by the extinction position would be observed.

Considering the autoradiographs of Plate 2 it is clear that polar growth of the coleoptile parenchyma does not occur and, as already pointed out, the apparently completely uniform incorporation of the radioactive glucose is not consistent with the concept of tip growth (Mühlethaler 1950) or with the view previously supported (Wardrop 1955) that the pit fields represent centres of cellulose synthesis, although the results do not completely exclude such a possibility. In addition, in Plate 2, Figure 3, it can be seen that, since the secondary thickenings in the cell wall (longitudinally oriented microfibrils) also contain radioactive cellulose, relative movement between microfibrils must also be involved in these regions. Such a result would suggest that the problem of extension growth in relation to secondary wall formation might be re-examined in other cases such as the surface growth involved in the differentiation of wood fibres (Wardrop 1954).

From Plate 2, Figure 5, it can be seen further that in epidermal parenchyma of coleoptiles incorporation of glucose into the cellulosic fraction of the cell wall also takes place uniformly and that tip growth is not involved, as indeed the measurements of Castle (1955) have already indicated. Here, too, secondary thickening on the outer surface does not appear to impede extension growth.

Accepting the view that the concept of multi-net growth is valid for coleoptile parenchyma, and so far as can be seen on the basis of autoradiographs of the cells cellulose is formed uniformly over the cell surface, the question arises of the factors which govern the initially transverse orientation of the microfibrils. It will be appreciated that once deposited in this orientation the subsequent disorientation of the microfibrils takes place in a manner consistent with stretching of the wall, although, as the evidence of Ordin, Cleland, and Bonner (1955) suggests, this may be facilitated by changes in some fractions of the non-cellulosic cell wall constituents. Thus the microfibrils on the inner surface of the wall maintain their orientation irrespective of the amount of cell extension and simultaneously with the disorientation of the microfibrils previously formed. This being so, it would seem that the mechanism of orientation of the microfibrils must depend initially on the organization of the protoplast at the interface between the wall and the protoplast. When surface growth occurs, however, the nature of disorientation of the microfibrils from the transverse direction would be expected to be a function of the polarity and extent of the surface enlargement which takes place.

Attention has been drawn previously (Wardrop 1954, 1955) to the fact that, in elongated parenchyma such as that in coleoptiles and in the petiole of *Narcissus*, the pit fields are transversely elongated, but in the former case they become more rounded as extension growth proceeds, whereas in the more or less isodiametric storage parenchyma of potatoes and apples the pit fields are nearly circular. These observations of the changes in the form of the pit fields may be interpreted as reflecting the difference in polarity of growth in the elongated and isodiametric parenchyma and its consequent modification of the pattern of the microfibrils. In this sense, the "tube texture" and "foliar texture" of Frey-Wyssling (1930) is seen as resulting from the difference in cell form.

Experimental modification of cell form leading to similar changes in the final microfibril texture of the cell wall was achieved by treatment of onion roots with colchicine. From Plate 4, Figures 1 and 2, it can be seen that cells from colchicine-treated roots are both shorter and broader than those from a normal root the same distance from the tip. An electron micrograph of a normal cell is shown in Plate 4, Figure 3, in which the usual disorientation of microfibrils on the outer surface can be seen. In Plate 4, Figure 4, is shown part of the outer surface of a colchicine-treated cell similar to those in Plate 4, Figure 2. In these cells which were shorter and broader than those from the normal roots (Plate 4, Fig. 1) it can be seen that the initial transverse orientation of the microfibrils tended to be maintained in the outer surface. This may be regarded as further evidence consistent with the view that the amount of disorientation of the microfibrils which takes place during surface growth is a function of both its extent and polarity.

IV. Acknowledgments

The author is indebted to Miss E. Sherriff, of the Commonwealth X-ray and Radium Laboratory, for great assistance in preparing the autoradiographs shown in Plate 2; and to Mr. A. M. Downes and Mr. K. R. Lynn, of the Tracer Elements Laboratory, C.S.I.R.O., for obtaining and storing the radioactive glucose used. He is also indebted to Professor James Bonner, of the California Institute of Technology, for suggestions and advice relating to the observations recorded in Table 1, and for helpful comment during the course of the investigation.

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Explanation of Plates 1–4

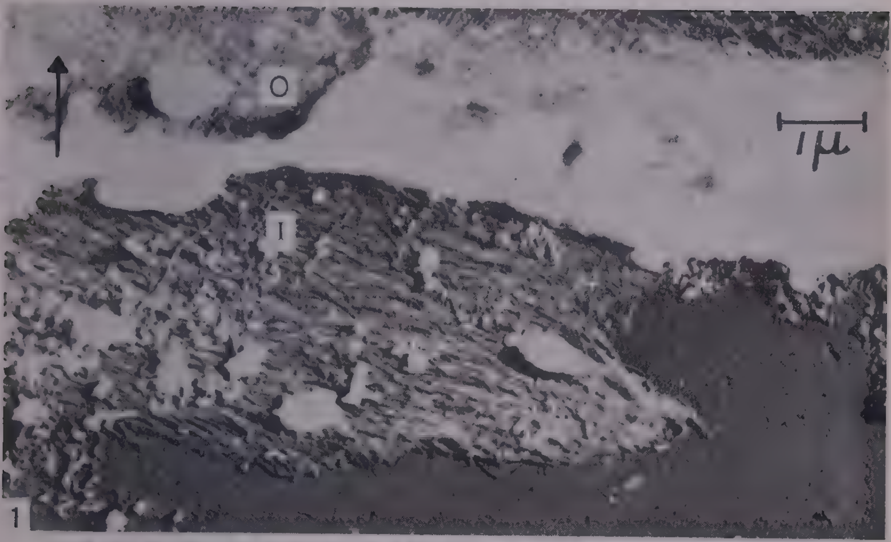
All electron micrographs shown in Plates 1, 3, and 4 were obtained after the specimens had been shadow cast with uranium. Arrows indicate the major morphological cell axis.

Plate 1

Fig. 1.—An electron micrograph of parenchyma from an *Avena* coleoptile showing the almost transverse orientation of microfibrils on the inner surface (I) compared with the more dispersed orientation on the outer surface (O) of the cell wall. ×12,000.

Fig. 2.—An electron micrograph of parenchyma 2 mm from the tip of an onion root showing the different orientation of microfibrils on the inner (I) and outer (O) surfaces. ×12,000.

SURFACE GROWTH IN PLANT CELLS



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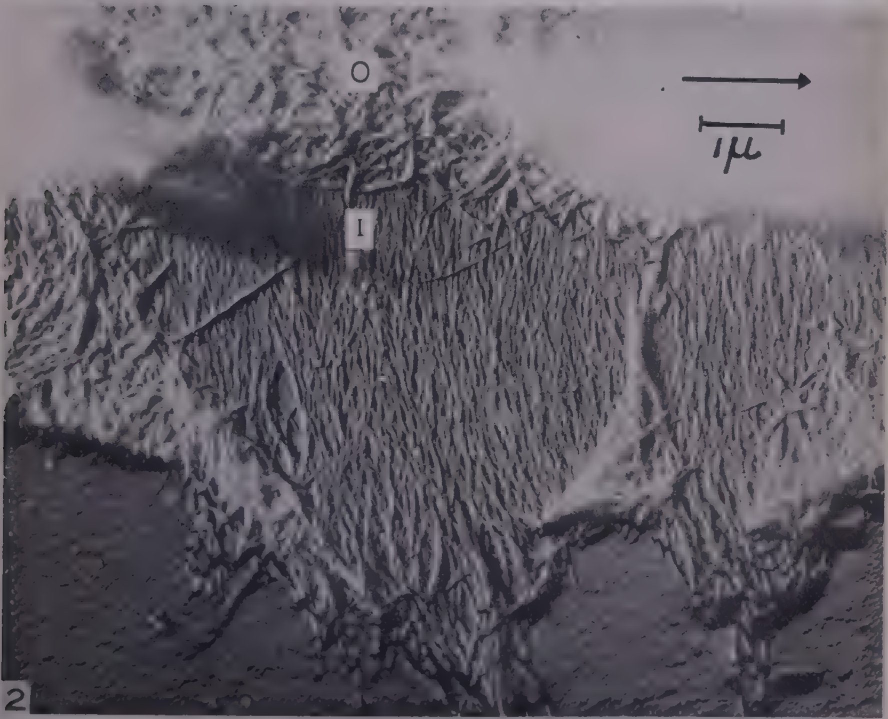

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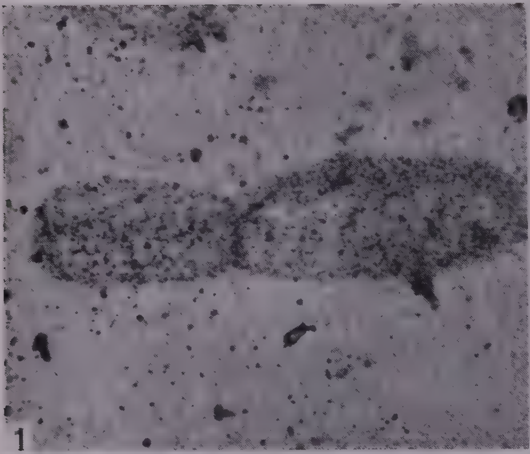

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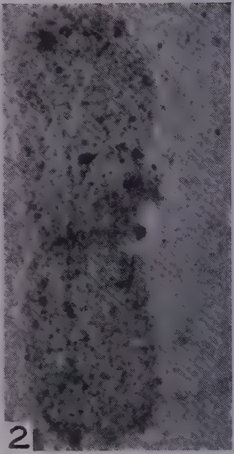

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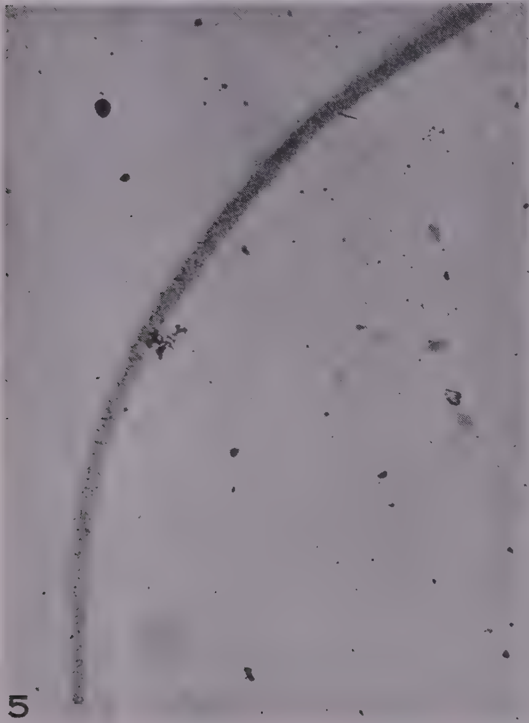

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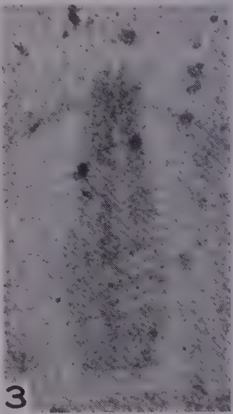

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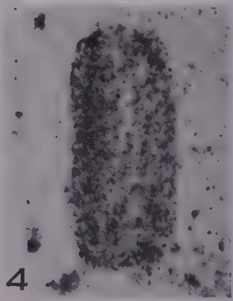

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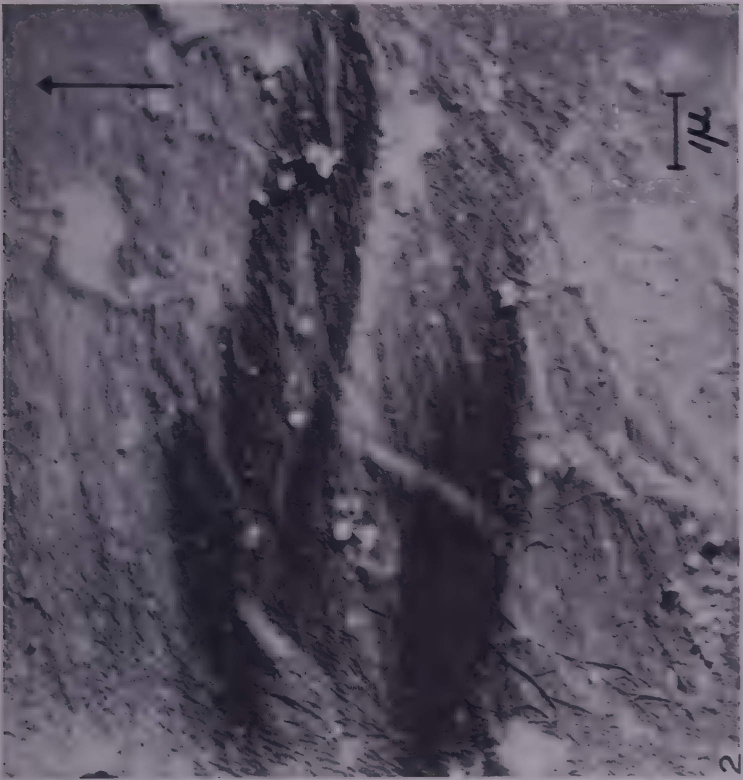

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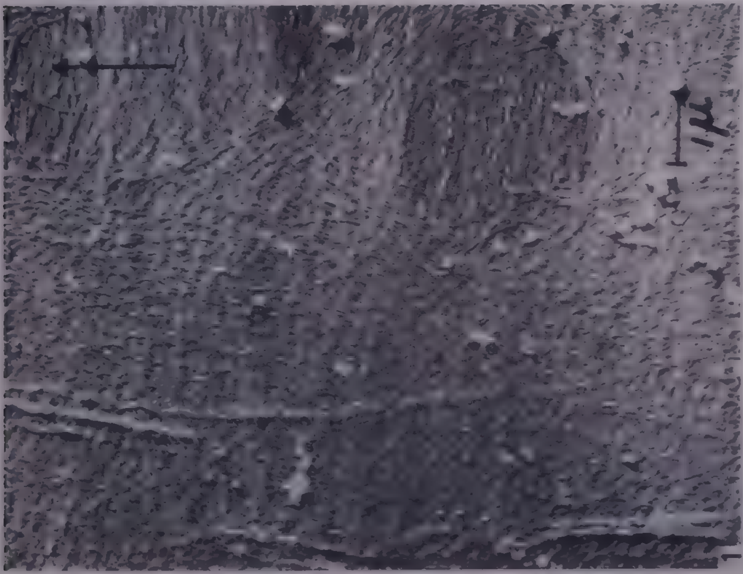

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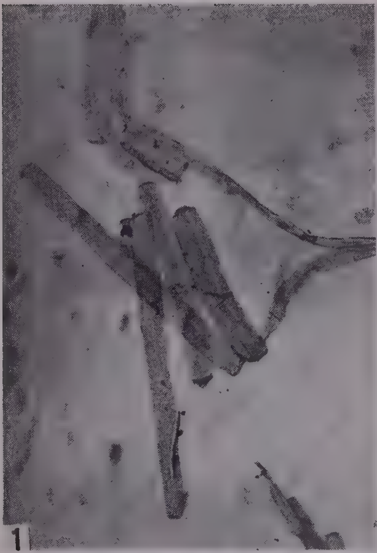
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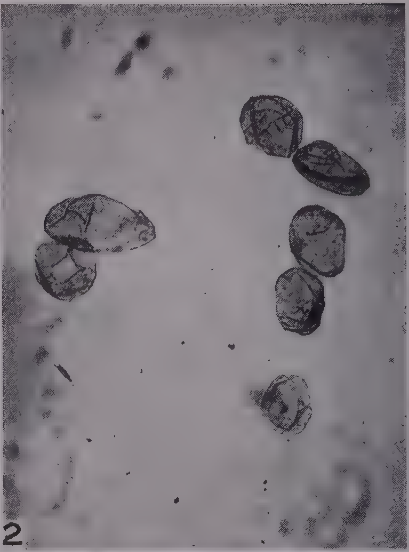
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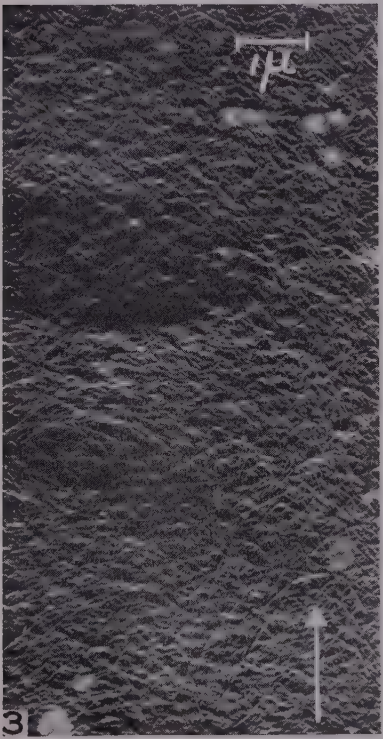

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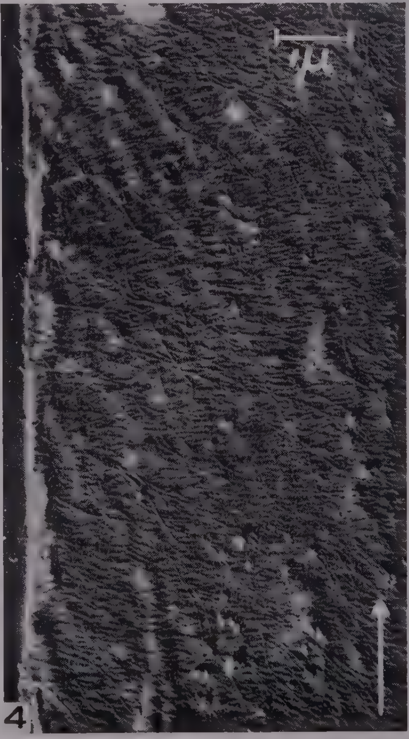

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PLATE 2

Figs. 1–4.—Autoradiographs of sub-epidermal parenchyma of *Avena* coleoptile segments after growing 12 hr in solutions containing labelled glucose. Note the uniform incorporation of radioactive material. In Figure 3 bands of secondary thickening are apparent. ×270.

Fig. 5.—An autoradiograph of an epidermal cell of *Avena* coleoptile segment after growing 12 hr in a solution containing labelled glucose. Note the band of secondary thickening on the outer surface of the cell. ×100.

PLATE 3

Fig. 1.—An electron micrograph of part of a parenchyma cell from an *Avena* coleoptile segment after growing 16 hr in a medium containing 1 per cent. sucrose plus 3-indoleacetic acid (1 mg/l). ×9300.

Fig. 2.—An electron micrograph of part of a parenchyma cell from an *Avena* coleoptile segment grown in a medium the same as that referred to in Figure 1 but with the addition of mannitol (0·35M). ×10,000.

PLATE 4

Fig. 1.—Parenchyma isolated from a point 2 mm from the tip of onion roots grown in water. ×100.

Fig. 2.—Parenchyma isolated from a point 2 mm from the tip of onion roots grown in 1 per cent. colchicine. ×100.

Fig. 3.—An electron micrograph of part of parenchyma cell from onion root grown in water, and corresponding to Figure 1. ×10,000.

Fig. 4.—An electron micrograph of part of the cell wall of a parenchyma cell similar to those shown in Figure 2. ×9000.

THE ANATOMY OF THE TIMBERS OF THE SOUTH-WEST PACIFIC AREA

V. FLACOURTIACEAE

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Summary

Examination of 13 genera from this area has indicated two structural groups within the timbers of the Flacourtiaceae. The wood anatomy of genera examined from areas other than the south-west Pacific area has been found to agree with these two groups.

The anatomical features of each genus have been summarized and salient features set out in tabular form. From these an artificial key separating the genera, where possible, has been prepared.

The grouping of the genera described based on wood anatomy is compared with the grouping of the family based on botanical features as suggested by Gilg (1925). Anatomical features separating the Flacourtiaceae from the groups of timbers with some similar characteristics have been indicated.

I. General

The Flacourtiaceae as understood by Gilg (1925) contains most of the genera included in the Bixineae and Samydaceae of Bentham and Hooker, and apart from one or two exceptions it is a fairly homogeneous group both botanically and on the basis of wood anatomy (see Section III for anatomical characters); the subdivision of the family used here is that accepted by Gilg and followed by Sleumer (1955) in his recent revision. The family is predominantly tropical or subtropical, containing about 84 genera, most of which are shrubs or trees. A few of the genera produce edible fruit, e.g. *Flacourtia indica* (Governor's plum), and the seeds of *Hydnocarpus kurzii* contain chaulmoogra oil, derivatives of which are used in the treatment of leprosy. One widely known timber produced by the family is "West Indian boxwood" or "zapatero" (*Gossypiospermum praecox* (Gris.) P. Wilson from Venezuela) which has been used to a large extent as a substitute for European boxwood in the manufacture of engravers' blocks, rulers, etc., and several other timbers have a limited local use, e.g. *Homalium tomentosum* (Vent.) Benth. (Burma lancewood). In the south-west Pacific area the most important timber-producing genera are *Homalium* and *Hydnocarpus*, and, to a lesser extent, *Trichadenia*, *Pangium*, *Ryparosa*, and *Casearia*. The anatomical descriptions are of genera from this area only, but species of the same genera available for examination from America, Africa, and India were also considered (see Section III). A number of genera not occurring in the south-west Pacific area were examined for purposes of comparison (see Appendix I). The distribution of the genera described is shown in Figure 1; this coverage of genera is by no means comprehensive, but it includes all from this area likely to be used for timber.

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II. Anatomical Characteristics of Genera Examined

All available wood specimens of each species were examined macroscopically and microscopically; the results were summarized and used for the preparation of the generic descriptions. Differences between the genera are set out in a key (Table 1) and in Table 2. Both in the generic descriptions and in Table 2, averages of the frequency of vessels, maximum vessel diameter, vessel member length, ray number, and fibre length have been recorded; because of variations within a tree, within a species, and between species, these measurements are not necessarily helpful in separating the genera, although certain trends can be observed.

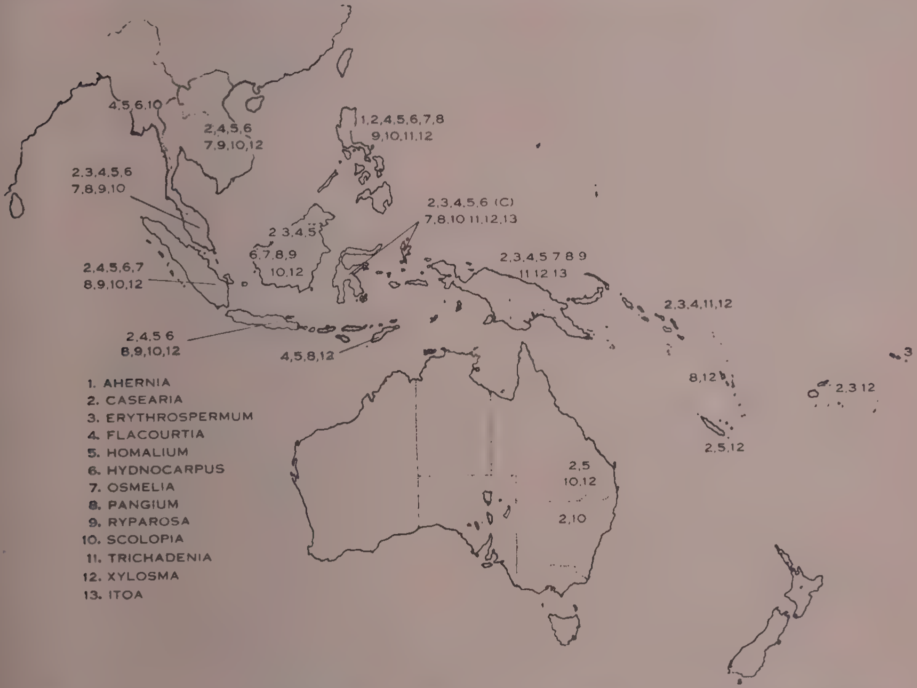

Fig. 1.—Distribution of genera of Flacourtiaceae examined from the south-west Pacific area.

The frequency of vessels was obtained from cross sections of each specimen and was calculated by counting the number of vessels in an area of about 50 sq. mm. The maximum tangential diameter of vessels was obtained for every specimen by making 20 measurements and averaging the 10 largest. Macerated material from each specimen was used for the measurement of vessel member length; 20 vessel members were selected at random and their lengths measured from tip to tip, the average for each specimen being thus obtained. The average ray number per millimetre for each specimen was obtained from the tangential section from 20 measurements of the number of rays intersected by a horizontal line 2 mm long. To determine average fibre length, measurements were made of 50 fibres taken at random from macerated material of mature wood. The approximate size of the intervascular pitting was estimated by measuring the vertical diameter of a number of individual pits in each specimen. The tangential diameters of the fibres were estimated from cross sections of each specimen. The fibre wall thickness recorded is the distance from the lumen of one cell to that of the next; it is considered that from a large number of such measurements a very close approximation to the thickness of two walls of one fibre is obtained. In the generic descriptions the ranges given for the above measurements are the ranges of the averages for individual wood specimens.

Table 1

GROUPING OF 13 GENERA OF THE FLACOURTIACEAE OCCURRING IN THE SOUTH-WEST PACIFIC AREA, BASED ON ANATOMICAL FEATURES*

A. Vessel-ray pits small, bordered, alternate; vertical diameter of intervascular pits 3–5 (occasionally 6) μ	*Casearia* *Flacourtia* *Homalium* *Osmelia* *Scolopia*
B. Vessel-ray pits apparently simple, rounded or gash-like or both; vertical diameter of intervascular pits mostly 7–10 μ (occasionally as low as 6 μ)	
(*a*) Perforation plates all or mainly simple	
(i) Rays 12–13/mm	
1. Upright ray cells sharply defined from procumbent; small uniseriate rays common	*Ahernia* *Xylosma*
2. Upright ray cells not sharply defined from others; central ray cells not always markedly procumbent; small uniseriate rays lacking	*Trichadenia*
(ii) Rays 6–9/mm	
1. Parenchyma plentiful	*Pangium*
2. Parenchyma absent or sparse	*Pangium* *Ryparosa*
(*b*) Perforation plates all multiple	
(i) Rays 7–9/mm; small uniseriate rays common consisting of markedly upright cells	*Erythrospermum*
(ii) Rays 12–18/mm; small uniseriate rays uncommon, cells not markedly upright	*Hydnocarpus*

* *Itoa:* material forwarded as belonging to this genus has not been included in the above key. This material can be recognized by the following features: (i) septate fibres only sporadic in occurrence; (ii) paratracheal parenchyma plentiful; (iii) intervascular pits coarse (10 μ × 12–14 μ).

(*a*) *Ahernia*

(i) *General.*—A monotypic genus of small trees occurring in Hainan and the Philippines and growing in primary forests up to about 2000 ft (Sleumer 1955); wood pale yellow-brown in colour, growth rings not distinct; texture moderately fine.

(ii) *Structure.*—*Vessels* numbering 26/sq. mm; 21 per cent. solitary, remainder in radial multiples up to 4 or 5; small, indistinct to the naked eye, average maximum

TABLE 2

SUMMARY OF ANATOMICAL CHARACTERISTICS OF 13 GENERA OF THE FLACOURTIACEAE OCCURRING IN THE SOUTH-WEST PACIFIC AREA

Genera	Vessels					Rays				Fibres		
	Vertical Diameter of Intervascular Pits (μ)	Average Maximum Tangential Diameter (μ)	Pore Number (No./sq. mm)	Vessel Member Length (mm)	Multiple Perforation Plates	Vessel-ray Pits Small, Bordered, Alternate	Ray Number (No./mm)	Ray Width (No. of cells)	Parenchyma Present	Tangential Diameter of Fibres (μ)	Fibre Length (mm)	Silica Present
Group I												
Casearia	3–4(5)	59–129	26–52(86)	0·5–1·4	—	+	10–18	1–4(7)	∓	20–40	1·1–2·1	—
Flacourtia	4–5	66–122	20–50	0·6–1·0	—	+	17–22	1–4	∓	20–30	1·1–1·8	—
Homalium	3–4(5)	64–155	18–99	0·5–1·5	—	+	11–19	1–5	∓	20–30	1·1–2·1	—
Osmelia	3–4	93–115	35–40	1·4–1·6	—	+	12–13	1–5	—	20–35	2·1–2·2	—
Scolopia	4–6	68–97	33–64	0·7–1·0	—	+	17–23	1–3(4)	—	20–30	1·2–1·8	—
Group II												
Ahernia	6–7	134	26	1·0	—	—	14	1–5	—	25–35	1·7	—
Erythrospermum	8–9	110–120	35–39	1·9–2·3	+	—	7–9	1–6	—	30–40	2·4–2·8	—
Hydnocarpus	7–11	64–165	16–77	1·3–2·5	+	—	12–18	1–3(4)	—	30–50	1·9–3·5	+
Pangium	8–10(11)	164–231	7–20	0·8–1·2	∓	—	6–9	1–5(7)	+	30–50	2·1–2·8	—
Ryparosa	7–8	159	13	2·2	—	—	7	1–5	—	40–50	3·7	—
Trichadenia	7–9	151–192	6–12	1·1–1·3	—	—	12–13	1–3(5)	+	30–40	2·2–3·0	—
Xylosma	8–10	88	41	1·1	—	—	14	1–4	—	20–30	1·7	—
Itoa	10	141–148	12	0·7–0·9	—	—	9–10	1–3	+	30–40	1·5–1·6	—

+ Present in most samples of the genus. ∓ Present in very few samples of the genus. — Not observed in any samples of the genus.

tangential diameter 134 μ; vessel member length 1·0 mm; intervascular pitting alternate, intermediate in size (diameters 6–7 μ); perforation plates simple; fine spirals sometimes visible in the extreme tips of the vessel members; no tyloses; no deposits. *Parenchyma* absent. *Rays* up to 4 or 5 cells wide; 14/mm; moderately high and heterogeneous with several (up to 9) marginal rows of upright cells; terminally confluent; vessel-ray pitting coarse, half-bordered but apparently simple with large apertures usually extended horizontally, scalariform in arrangement; crystals abundant, predominantly in the upright cells and uniseriate rays where they may be chambered, but also present in the procumbent cells. *Fibres* thin-walled, wall narrower than the lumen; length 1·7 mm; diameters 25–35 μ; all fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls.

(iii) *Material.*—*Ahernia glandulosa* Merr., one sample, Philippine Is.

(*b*) *Casearia*

(i) *General.*—A genus of approximately 160 species of small trees or shrubs distributed in tropical and subtropical regions (Sleumer 1955), growing mostly in lowland rain-forests, but also in mountain forests. The majority of wood specimens examined were pale yellow or pale brown in colour, pinkish tints being absent in almost all cases; two unidentified species (Queensland, North Borneo) were a moderately dark brown; growth rings not distinct; texture fine or moderately fine; grain usually straight and fissile; air-dry density 40–60 lb/cu. ft; pith flecks occasionally present.

(ii) *Structure* (Plate 1, Fig. 1; Plate 2, Fig. 3; Plate 3, Fig. 4).—*Vessels* numbering 26–52/sq. mm, but 86/sq. mm in *C. multinervosa*; 20–57 per cent. solitary, remainder in radial multiples usually up to 3 or 4, but in some samples up to 6 or 7; small or very small, indistinct or sometimes invisible to the naked eye, average maximum tangential diameter 59–129 μ; vessel member length 0·5–1·4 mm; intervascular pitting alternate, small or minute (3–4 occasionally 5 μ diameter); perforation plates simple; no tyloses; deposits usually absent. *Parenchyma* absent or very sparse, paratracheal; crystals observed in one sample. *Rays* usually 1–4, occasionally up to 5 or 7 cells wide; 10–18/mm; often high and always heterogeneous with long uniseriate margins consisting of upright cells; central cells often not markedly procumbent; slight disjunctive tendency in the marginal cells of some samples; vessel-ray pitting small and similar to the intervascular, with a tendency to be unilaterally compound in some samples; crystals usually plentiful, but apparently absent in a few samples, occurring throughout the rays but sometimes more abundant and occasionally chambered in the upright cells; druses common in unspecialized cells in *C. fuliginosa* (Plate 3, Fig. 4). *Fibres* thin-walled to moderately thick-walled; wall narrower or wider than the lumen; length 1·1–2·1 mm; diameters 20–40 μ; all fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls.

(iii) *Material.*—*Casearia dallachyi* F. Muell., two samples, North Queensland; *C. fuliginosa* (Blanco) Blanco, one sample, Philippine Is.; *C. grewiifolia* Vent., five samples, New Guinea, New Britain, Admiralty Is.; *C. grewiifolia* Vent. var. *deglabrata* Koord. & Val., two samples, Philippine Is.; *C. multinervosa* C. T. White

& Sleum., one sample, New South Wales; *C. trivalvis* (Blanco) Merr., one sample, Philippine Is.; unassigned species, six samples, Admiralty Is., New Guinea, North Borneo, Queensland.

(c) *Erythrospermum*

(i) *General.*—A genus of small trees or shrubs comprising about five species, one of which occurs in Malaysia (Sleumer 1955); wood pale yellow in colour; growth rings not distinct; texture moderately fine; grain straight and fissile; density 39 lb/cu. ft.

(ii) *Structure* (Plate 2, Figs. 1 and 2; Plate 3, Fig. 6).—*Vessels* numbering 35–39/sq. mm; 59–62 per cent. solitary, remainder in radial multiples up to 2 or 3, occasionally more; small, indistinct to the naked eye, average maximum tangential diameter 110–120 μ; vessel member length 1·9–2·3 mm; intervascular pitting alternate with a tendency to an opposite arrangement in places, moderately coarse (diameters 8–9 μ); perforation plates all multiple with numerous moderately coarse to moderately fine bars; no tyloses; no deposits. *Parenchyma* absent. *Rays* up to 6 cells wide; 7–9/mm; high and heterogeneous with several rows of upright cells which may be slightly disjunctive, occurring at the margins of the rays or in uniseriate rays; vessel-ray pitting coarse, half-bordered but apparently simple with large apertures usually extended horizontally, scalariform in arrangement; crystals abundant, distributed throughout the rays. *Fibres* moderately thin-walled, wall mostly narrower than the lumen; length 2·4–2·8 mm; diameters 30–40 μ; all fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls.

(iii) *Material.*—*Erythrospermum candidum* (Becc.) Becc., two samples, New Guinea.

(d) *Flacourtia*

(i) *General.*—A genus of small trees and shrubs comprising about 15 species occurring in the warmer parts of Africa and Asia, extending to Polynesia (Sleumer 1955); wood pale yellow-brown to brown; growth rings not distinct; texture fine; grain may be somewhat interlocked and not very fissile; air-dry density approximately 54–57·5 lb/cu. ft.

(ii) *Structure* (Plate 3, Fig. 3).—*Vessels* numbering 20–50/sq. mm; 11–50 per cent. solitary, remainder in radial multiples up to 4, sometimes to 6 or 7; small or very small, indistinct or invisible to the naked eye, average maximum tangential diameter 66–122 μ; vessel member length 0·6–1·0 mm; intervascular pitting alternate, small (diameters 4–5 μ); perforation plates simple; no tyloses; resin deposits may be present. *Parenchyma* absent or sparse paratracheal, sometimes containing chambered crystals; resin deposits may be present. *Rays* up to 4 cells wide; 17–22/mm; heterogeneous with several (up to 12) marginal rows of upright cells; often terminally confluent; vessel-ray pitting small and similar to the intervascular; crystals common, sometimes chambered in the upright cells; resin deposits may be present. *Fibres* moderately thin to thick-walled, wall narrower or wider than the lumen; length 1·1–1·8 mm; diameters 20–30 μ; all fibres septate; pits small, numerous, indistinctly bordered; mainly on the radial walls; chambered crystals observed in *F. rukam* and *F. inermis* (Plate 3, Fig. 3).

(iii) *Material.—Flacourtia indica* (Burm. f.) Merr., one sample, Philippine Is., two samples, unrecorded localities; *F. inermis* Roxb., one sample, Philippine Is.; *F. rukam* Zoll & Mor., one sample, Philippine Is., one sample, unrecorded locality.

(*e*) *Homalium*

(i) *General.*—A genus of trees and shrubs, comprising about 180 species occurring in lowland rain-forests in most tropical countries (Sleumer 1955); wood varying in colour from pale yellow or pale yellow-brown to orange-brown or brown, sometimes with slightly pinkish tints; growth rings not distinct; texture fine or moderately fine; grain usually straight and fissile; air-dry density 45–60 lb/cu. ft.

(ii) *Structure* (Plate 2, Fig. 4).—*Vessels* numbering 18–99/sq. mm; 6–63 per cent. solitary, remainder in radial multiples usually up to 4 but may sometimes occur up to 6 or 8; usually small or very small, indistinct to the naked eye, average maximum tangential diameter 64–155 μ; vessel member length 0·5–1·5 mm; no tyloses; resin deposits occasionally present; intervascular pitting alternate, small or minute (diameters 3–4 occasionally 5 μ); perforation plates simple. *Parenchyma* absent, or very sparse paratracheal, which may occasionally contain crystals. *Rays* up to 5 cells wide; 11–19/mm; heterogeneous with several marginal rows of upright cells; often terminally confluent; vessel-ray pitting small and similar to the intervascular, occasionally with a tendency to be unilaterally compound; crystals abundant, mainly in the upright cells, sometimes chambered; resin deposits common in the more darkly coloured genera, especially in the procumbent cells. *Fibres* moderately thin to thick-walled, wall usually wider than the lumen; length 1·1–2·1 mm; diameters 20–30 μ; all fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls; crystals observed in the septate fibres in some samples of *H. foetidum*.

(iii) *Material.—Homalium bracteatum* Benth., one sample, Philippine Is.,; *H. circumpinnatum* Bail., five samples, Queensland; *H. foetidum* (Roxb.) Benth., 14 samples, Indonesia, North Borneo, New Guinea, Philippine Is.; *H. loheri* Merr., one sample, Philippine Is.; *H. oblongifolium* Merr., one sample, Philippine Is.; *H. panayanum* F.-Vill., one sample, Philippine Is.; *H. villarianum* Vid., one sample, Philippine Is.; *H. vitiense* Benth., two samples, Queensland; unassigned species, two samples, Burma, Philippine Is.

(*f*) *Hydnocarpus*

(i) *General.*—A genus of trees and shrubs comprising about 40 species most of which occur in lowland rain-forests in the Malaysian and south-east Asian areas as far west as India (Sleumer 1955); all wood samples examined were pale yellow in colour; growth rings not distinct; texture intermediate to fine; grain straight and fissile; air-dry density 44–50 lb/cu. ft.

(ii) *Structure* (Plate 3, Figs. 5 and 7).—*Vessels* numbering 16–77/sq. mm; 20–40 per cent. solitary, remainder in radial multiples mostly up to 3 or 4, occasionally to 6 or 7; small, indistinct to the naked eye, average maximum tangential diameter 64–165 μ; vessel member length 1·3–2·5 mm; intervascular pitting moderately coarse (diameters 7–11 μ) and alternate with a slight tendency to an opposite arrangement; perforation plates multiple with many coarse bars; fine spirals occasionally visible in the extreme tips of the vessel elements; tyloses may be present; white deposits of vitreous silica are often visible in the vessels with the aid of a hand lens (Amos 1952). *Parenchyma* absent. *Rays* up to 3, occasionally 4 cells wide; 12–18/mm; high and heterogeneous with long uniseriate margins of square or slightly upright cells; central cells not markedly procumbent; vessel-ray pitting coarse, half-bordered but apparently simple with large apertures often extended horizontally, sometimes scalariform in arrangement; crystals commonly (but not always) present, especially in the central cells; silica present in *H. sumatrana*. *Fibres* thick to very thick-walled, wall wider than the lumen; length 1·9–3·5 mm; diameters 30–50 μ; all fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls; silica present in *H. sumatrana* (Plate **3**, Fig. 7).

(iii) *Material.—Hydnocarpus heterophylla* Bl., two samples, Philippine Is.; *H. kunstleri* (King) Warb., one sample, Malaya; *H. kunstleri* (King) Warb. var. *tomentosa* (King) Sleum., two samples, Malaya; *H. subfalcata* Merr., one sample, Philippine Is., *H. sumatrana* (Miq.) Koord., one sample, Philippine Is.; *H. woodii* Merr., one sample, Malaya; unassigned species, one sample, Philippine Is.

(*g*) *Osmelia*

(i) *General.*—A genus of small trees comprising four species, three of which occur throughout Malaysia, and one in Ceylon; mostly at low altitudes (Sleumer 1955); wood pale yellow in colour; growth rings not distinct; texture fine.

(ii) *Structure.—Vessels* numbering 35–40/sq. mm; 16–43 per cent. solitary, remainder in radial multiples up to 3–5; small to very small, indistinct or invisible to the naked eye, average maximum tangential diameter 93–115 μ; vessel member length 1·4–1·6 mm; intervascular pitting alternate, small or minute (diameters 3–4 μ); perforation plates simple; no tyloses; no deposits. *Parenchyma* absent. *Rays* uniseriate and up to 3 or 5 cells wide with a slight tendency for two distinct widths; 12–13/mm; markedly heterogeneous with several (up to 10) marginal rows of high upright cells; central ray cells may not be markedly procumbent; vessel-ray pitting small and similar to the intervascular type; crystals common, occurring all through the rays or sometimes tending to be concentrated in the central cells. *Fibres* thick or moderately thick-walled; wall as wide or wider than the lumen; length 2·1–2·2 mm; diameters 20–35 μ; all fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls.

(iii) *Material.—Osmelia philippina* (Turcz) Benth., two samples, Philippine Is.

(*h*) *Pangium*

(i) *General.*—A monotypic genus occurring throughout Malaysia and extending to Melanesia and Micronesia (Sleumer 1955); trees scattered through rain-forest areas; wood pale yellow in colour; growth rings not distinct; texture coarse or moderately coarse; grain usually straight and fissile; air-dry density 33–42 lb/cu.ft.

(ii) *Structure* (Plate 1, Fig. 3; Plate 3, Fig. 1).—*Vessels* numbering 7–20/sq. mm; 17–55 per cent. solitary, remainder in radial multiples up to 3 or 4, occasionally to 6; small to intermediate in size, usually visible to the naked eye, average maximum tangential diameter 164–231 μ; vessel member length 0·8–1·2 mm; intervascular pitting moderately coarse (diameters usually 8–10 μ), alternate in arrangement; perforation plates almost entirely simple, occasional multiple perforation plates present with numerous fine bars; no tyloses; no deposits. *Parenchyma* variable in quantity from sparse paratracheal to abundant paratracheal, usually with a few scattered diffuse strands; crystals usually present. *Rays* up to 5, occasionally 6–7 cells wide; 6–9/mm; usually 2–4 mm high; the distinction between upright and procumbent cells is not as marked as in other members of the family, however the rays may contain several marginal rows of squarish or slightly upright cells; vessel-ray pitting coarse, half-bordered but apparently simple with large apertures often extended horizontally, sometimes tending to a scalariform arrangement; crystals present throughout the rays, variable in quantity. *Fibres* moderately thin to moderately thick-walled, wall usually as wide or wider than the lumen; length 2·1–2·8 mm; diameters 30–50 μ; fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls.

(iii) *Material.*—*Pangium edule* Reinw., 11 samples, Malaya; New Guinea, Philippine Is.

(*i*) *Ryparosa*

(i) *General.*—A genus of rain-forest trees or rarely shrubs comprising about 18 species occurring throughout Malaysia extending to Siam and the Andamans (Sleumer 1955); wood pale yellow in colour; growth rings not distinct; texture moderately coarse; grain straight and fissile.

(ii) *Structure.*—*Vessels* numbering 13/sq. mm; 17 per cent. solitary, remainder in radial multiples up to 3; small to intermediate in size, indistinct to the naked eye, average maximum tangential diameter 159 μ; vessel member length 2·2 mm; intervascular pitting moderately coarse (diameters 7–8 μ), alternate in arrangement; perforation plates simple, no multiple being observed; tyloses common; no deposits. *Parenchyma* absent. *Rays* up to 4–5 cells wide; 7/mm; high (up to 4–6 mm) and heterogeneous with long uniseriate margins consisting of square or slightly upright cells; vessel-ray pitting coarse, half-bordered but apparently simple with large apertures extended horizontally, scalariform in arrangement; crystals not abundant, distributed throughout the rays. *Fibres* moderately thick-walled, wall usually wider than the lumen; length 3·7 mm; diameters 40–50 μ; septa present; pits small, numerous, indistinctly bordered, mainly on the radial walls.

(iii) *Material.*—One sample only, species unassigned, New Guinea.

(*j*) *Scolopia*

(i) *General.*—A genus of small trees or shrubs comprising about 40 species occurring in tropical and subtropical Africa, India, and south-east Asia, extending to Queensland and New South Wales; scattered in primary and secondary forests at low and medium altitudes (Sleumer 1955); wood pale or definite brown in colour, sometimes with pinkish tints; growth rings not distinct; texture fine; grain usually straight and fissile; air-dry density 44–62 lb/cu. ft.

(ii) *Structure* (Plate 1. Fig. 2).—*Vessels* numbering 33–64 sq. mm; 29–38 per cent. solitary, remainder in radial multiples up to 4 or 7; small or very small, usually invisible to the naked eye, average maximum tangential diameter 68–97 μ; vessel member length 0·7–1·0 mm; intervascular pitting alternate, small or very small (diameters 4–6 μ); perforation plates simple; no tyloses; resin deposits occasionally present. *Parenchyma* absent; pith flecks observed in one sample. *Rays* usually 1–3, sometimes to 4 cells wide; 17–23 mm; moderately high and heterogeneous with long uniseriate margins consisting of several rows of upright cells; vessel-ray pitting similar to the intervascular, sometimes with relatively large apertures; crystals common, sometimes abundant, occurring throughout the rays, but usually more abundant and chambered in the upright cells; horizontal rows of chambered crystals observed in the procumbent cells of one specimen of *S. spinosa*; resin may be abundant especially in the procumbent cells. *Fibres* moderately thin to thick-walled; length 1·2–1·8 mm; diameters 20–30 μ; all fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls; chambered crystals observed in the fibres of *S. spinosa* and *S. luzonensis*; resin deposits sometimes present.

(iii) *Material.—Scolopia brownii* F. Muell., two samples, New South Wales; *S. luzonensis* (Presl.) Warb., one sample, Philippine Is.; *S. spinosa* (Roxb.) Warb., two samples, North Borneo, Philippine Is.

(k) *Trichadenia*

(i) *General.*—A genus of two species, one occurring in Ceylon, the other in Eastern Malaysia extending to the Philippine Is. and New Britain, growing in primary or old secondary forests in level or hilly, never inundated localities (Sleumer 1955); wood pale yellow in colour; growth rings not distinct; texture moderately coarse; grain usually straight and fissile; air-dry density 50–60 lb cu. ft.

(ii) *Structure* (Plate 1, Fig. 4; Plate 3, Fig. 2).—*Vessels* numbering 6–12 sq. mm; 15–28 per cent. solitary, remainder in radial multiples up to 3 or 4, occasionally 5; small to intermediate in size, usually indistinct to the naked eye, average maximum tangential diameter 151–192 μ; vessel member length 1·1–1·3 mm; intervascular pitting moderately coarse (diameters 7–9 μ), alternate in arrangement; perforation plates simple, no multiple perforation plates observed; tyloses occasionally present; deposits absent. *Parenchyma* sparse or very sparse paratracheal, occasionally with a few diffuse cells; a few crystals observed in one sample. *Rays* usually 1–3, occasionally up to 5 cells wide; 12–13 mm; high (up to 8 mm) and terminally confluent; the distinction between upright and procumbent cells is not as marked as is common for the family, but several marginal rows of slightly upright cells may be present; vessel-ray pitting coarse, half-bordered but apparently simple with large apertures sometimes extended horizontally; crystals plentiful throughout the rays; resinous deposits may be present. *Fibres* thick to very thick-walled, wall wider than the lumen; length 2·2–3·0 mm; diameters 30–40 μ; all fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls.

(iii) *Material.—Trichadenia philippinensis* Merr., six samples, New Guinea, Solomon Is., Philippine Is.

(*l*) *Xylosma*

(i) *General.*—A genus of trees or shrubs comprising about 104 species distributed throughout the tropics, Africa excepted; occurring in Malaysia in rain-forests, sometimes in the montane zone (Sleumer 1955); wood varying in colour from pale yellow to pale brown, with pink tints; growth rings not distinct; texture fine; grain straight and fissile.

(ii) *Structure.*—*Vessels* numbering 41/sq. mm; 29 per cent. solitary, remainder in radial multiples up to 6–9; small to very small, indistinct or invisible to the naked eye, average maximum tangential diameter 88 μ; vessel member length 1·1 mm; intervascular pitting moderately coarse (diameters 8–10 μ) and alternate in arrangement; perforation plates simple; fine spirals observed in the tips of the vessel members of *X. sumatranum*; no tyloses; no deposits. *Parenchyma* absent. *Rays* up to 4 cells wide; 14/mm; moderately high and heterogeneous with several marginal rows of upright cells; vessel-ray pitting half-bordered but apparently simple with large round apertures; crystals common, distributed throughout the rays, sometimes chambered in the upright cells. *Fibres* moderately thin-walled, wall usually narrower than the lumen; length 1·7 mm; diameters 20–30 μ; all fibres septate; pits small, numerous, indistinctly bordered, mainly on the radial walls.

(iii) *Material.*—*Xylosma sumatranum* Sloot., one sample, New Guinea.

(*m*) *Itoa*

It should be noted that the wood anatomy of this genus differs in certain respects from other members of the family and is dealt with separately.

(i) *General.*—A genus comprising two closely allied species, both trees, one in south China and Indo-China (*I. orientalis* Hemsl.) and the other in Celebes, Moluccas, and New Guinea; scattered in old mixed primary and in secondary rain-forests in level, sometimes inundated, or hilly localities (Sleumer 1955); heartwood of a definite brown colour, sapwood pale straw; growth rings not distinct; texture intermediate; grain straight and fissile; air-dry density 33–37 lb/cu. ft.

(ii) *Structure.*—*Vessels* numbering 12/sq. mm; 37–41 per cent. solitary, remainder in radial multiples mostly up to 4 but occasionally more (6 or 7) due to small pores associated with the large; clusters present; small, indistinct to the naked eye, average maximum tangential diameter 141–148 μ; vessel member length 0·7–0·9 mm; intervascular pitting alternate, moderately coarse (diameters about 10 μ); perforation plates simple; fine spirals sometimes visible in the extreme tips of the vessel members; no tyloses; no deposits. *Parenchyma* moderately plentiful paratracheal, sometimes with a slight aliform tendency; crystals present. *Rays* up to 3 cells wide; 9–10/mm; heterogeneous with several (to 6 or 8) marginal rows of upright or squarish cells; may be terminally confluent; vessel-ray pitting coarse, half-bordered but apparently simple with large apertures often extended horizontally, scalariform in arrangement; crystals abundant, predominantly in the marginal cells. *Fibres* thin-walled; wall narrower than the lumen; length 1·5–1·6 mm; diameters 30–40 μ; septate fibres present, but only sporadic in occurrence; pits small, moderately numerous, indistinctly bordered, mainly on the radial walls.

(iii) *Material.*—*Itoa stapfii* (Koord.) Sleum., two samples, New Guinea.

III. Discussion

The timbers of this family have a characteristic anatomical structure, which may be summarized as follows:

Vessels.—Radial multiples always present, intervascular pitting usually alternate, but sometimes with a tendency to an opposite arrangement in *Erythrospermum* and *Hydnocarpus*, not vestured; perforation plates simple in most genera examined, but multiple in *Erythrospermum*, *Hydnocarpus*, *Scottellia*, and very occasionally in *Pangium*; siliceous inclusions usually absent, but usually present in the vessels of *Hydnocarpus* (Amos 1952) and also in the ray cells and fibres of *Hydnocarpus sumatrana* (Plate 3, Fig. 7); of the genera examined from outside the south-west Pacific area silica was present only in the ray cells of *Carpotroche amazonica*.

Parenchyma.—Absent or very sparse paratracheal, but more abundant in *Pangium*, *Itoa*, and sometimes *Trichadenia*; small quantities of diffuse may occur in *Pangium*.

Rays.—Often tall but not extremely so; frequently appearing very numerous with a high proportion of ray material on cross and tangential longitudinal sections; usually heterogeneous with long uniseriate margins consisting of upright cells; often terminally confluent; small uniseriate rays consisting of upright cells usually present but rare in *Hydnocarpus*, *Pangium*, *Ryparosa*, and *Trichadenia* (Plate 3, Figs. 1, 2, 5, 6); with the appearance of two distinct widths in occasional samples of *Casearia*, *Homalium*, *Osmelia*, and certain genera occurring outside the south-west Pacific area, e.g. *Ryania*; crystals distributed throughout the rays in nearly all genera, sometimes chambered in the upright cells; the type of crystal is not characteristic except in *Casearia fuliginosa* in which most of the crystals observed were in the form of small druses (Plate 3, Fig. 4).

Fibres.—Consistently septate except in *Itoa* (see Section II(*m*)), pits small, numerous, indistinctly bordered, mainly on the radial walls; chambered crystals observed in the septate fibres of some samples of *Homalium*, *Flacourtia*, and *Scolopia* (Plate 3, Fig. 3).

Within the framework of the above summary, the family can be divided into two well-defined groups. In one of these (hereafter called "Group I"), the timbers have small, bordered, alternate, vessel-ray pits (Plate 2, Fig. 3), associated with small to minute intervascular pitting, mostly 3–5 μ vertical diameter (Plate 2, Fig. 4), as in *Casearia*, *Flacourtia*, *Gossypiospermum*, *Homalium*, *Laetia*, *Osmelia*, *Ryania*, *Scolopia*, and *Zuelania*; the timbers of this group are very homogeneous as regards anatomical characters. In the other group (hereafter called "Group II"), the timbers have gash-like or rounded vessel-ray pitting (Plate 2, Fig. 2) associated with intermediate or moderately coarse intervascular pitting, mostly 7–11 μ vertical diameter (Plate 3, Figs. 2 and 5), as in *Ahernia*, *Carpotroche*, *Erythrospermum*, *Hasseltia*, *Hydnocarpus*, *Kiggelaria*, *Lindackeria*, *Pangium*, *Ryparosa*, *Scottellia*, *Trichadenia*, and *Xylosma*; the timbers of this group, however, are not very homogeneous in structure, and vary to a marked degree in such features as the presence of multiple perforation plates, presence of vertical parenchyma, abundance of small uniseriate rays, average dimensions of the fibres, and the degree of extension of the fibres from the cambial initials as estimated by the ratio of fibre length to vessel member length (Chalk and Chattaway 1934); *Pangium* in particular has a relatively high degree of extension of the fibres (fibre length 2·2–2·8 times the vessel member length) as well as differing from other Flacourtiaceae in the abundance of vertical parenchyma. *Itoa* is comparable to Group II, but differs in having only sporadic septate fibres, coarser intervascular pits (10 μ by 12–14 μ), and moderately plentiful paratracheal parenchyma.

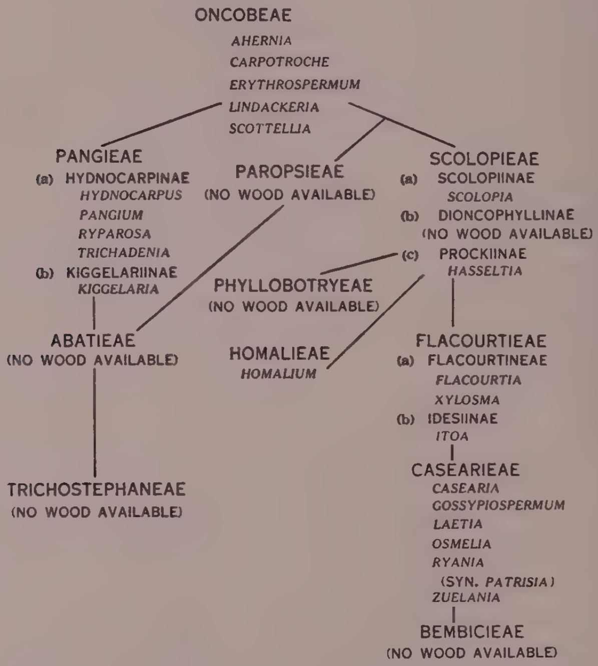

Fig. 2.—Grouping of the Flacourtiaceae on botanical features (from Gilg 1925) showing genera examined in this report.

Gilg (1925) has arranged the subdivisions of the family in a proposed phyletic sequence on the basis of botanical features as shown in Figure 2. From this arrangement it can be seen that the timbers of Group I correspond to the Scolopieae, Homalieae, Flacourtieae, and Casearieae, while the timbers of Group II correspond to the Oncobeae and Pangieae. On the basis of the wood anatomy of the samples examined, *Hasseltia*, *Xylosma*, and *Itoa* appear to be inconsistent as these genera do not correspond with any of the timbers in Group I, although botanically they have been placed in the Scolopieae and Flacourtieae respectively. Apparently there is a considerable amount of variation in the structure of different species of *Xylosma*, since both Record and Hess (1943) and Metcalfe and Chalk (1950) group this genus with genera corresponding to Group I. In this report the number of genera is too small to facilitate an effective comparison of the anatomy of the groups of the family. However, on the basis of other descriptions of members of this family

(Solereder 1908; Pearson and Brown 1932; Tupper 1934; Record and Hess 1943; Metcalfe and Chalk 1950) it appears that most genera can be assigned to one of the two anatomical groups indicated above, although inconsistencies do occur (e.g. *Ancistothyrsus*, *Peridiscus*, *Aphloia*, *Dioncophyllum*).

An artificial grouping of the genera examined, based on anatomical features of the wood is given in Table 1.

No consistent anatomical differences were found between *Casearia*, *Flacourtia*, *Homalium*, *Osmelia*, and *Scolopia*; in general the differences within the genera are as great as the differences between the genera. *Homalium foetidum* can be distinguished from *Casearia grewiifolia* by its darker colour and greater distinction between the upright and procumbent ray cells; as these are the most common timber species of each genus in certain areas, this distinction may be of some use, but, when the genera are considered as a whole, these differences do not hold. By reference to Table 2 it can be seen that minor differences occur in average vessel diameter, ray number, fibre length, etc.

Ahernia and *Xylosma* are similar in structural features; in the samples examined the vessel-ray pits of *Ahernia* were more gash-like in form than those of *Xylosma*. Table 2 indicates minor differences in the size and number of the vessels.

Pangium, *Ryparosa*, and *Trichadenia* are similar in structural features, *Trichadenia* differing in the height and number of the rays (Plate 3, Figs. 1 and 2); *Pangium* has more parenchyma than *Trichadenia* (Plate 1, Figs. 3 and 4), and no parenchyma was observed in *Ryparosa*; the vessel-ray pits of *Trichadenia* tend to be rounded rather than gash-like as in *Pangium* and *Ryparosa*; other minor differences between these genera are indicated in Table 2.

A few timbers have an anatomical structure which can be confused with that of the Flacourtiaceae. Most of the genera included in the Phyllanthoideae "B", and some of the Bridelieae, of the family Euphorbiaceae as arranged by Metcalfe and Chalk (1950) are similar to the timbers of Group II. In these cases, it is helpful to bear in mind the almost universal presence of crystals in the rays of the Flacourtiaceae; also the type of crystal is sometimes of use, for example, the elongated crystals characteristic of the fibres and ray cells of *Glochidion* do not occur in the Flacourtiaceae. The genera of the Bridelieae are reported (Metcalfe and Chalk 1950) to have vestured pits—again a feature which does not occur in the Flacourtiaceae. One group of the Apocynaceae, and one group of the Rubiaceae are characterized by septate fibres, lack of parenchyma, and vessel-ray pits similar to the intervascular type, but can be distinguished from Group I of the Flacourtiaceae by the presence of vestured pits. Some samples of *Siphonodon* of the Celastraceae are similar to Group I, but can usually be distinguished by the presence of large crystals in slightly enlarged cells near the margins of the rays.

IV. ACKNOWLEDGMENTS

Material used in this survey was taken from the standard collection of the Division of Forest Products. Special references must be made to specimens from New Guinea and neighbouring islands received from Mr. J. B. McAdam, Director of the Department of Forests of the Papua–New Guinea Administration; to speci-

mens from New Guinea sent by Dr. R. D. Hoogland, of the Land Research and Regional Survey Section, C.S.I.R.O.; to specimens from the Philippine Is. sent by Mr. F. N. Tamolang, Wood Technologist of the Forest Products Laboratory College, Laguna, Los Banos; to specimens from the British Solomon Is., collected by Mr. F. S. Walker in 1945 and 1946; to specimens from North and South America supplied on an exchange basis by Dr. C. C. Gregg, Director of the Natural History Museum, Chicago, U.S.A., and Dr. B. Francis Kukachka of the Forest Products Laboratory, Madison, U.S.A.

Material received from the Forest Department of the Papua–New Guinea Administration was originally identified botanically by Mr. J. S. Womersley, Chief, Division of Botany, Department of Forests, New Guinea, that from the British Solomon Is. (collected by Mr. F. S. Walker) by the late Mr. C. T. White, Government Botanist, Brisbane.

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Explanation of Plates 1–3

Plate 1

Fig. 1.—*Casearia grewiifolia* Vent. Transverse section. ×25.

Fig. 2.—*Scolopia brownii* F. Muell. Transverse section. ×25.

Fig. 3.—*Pangium edule* Reinw. Transverse section showing paratracheal and diffuse parenchyma. ×25.

Fig. 4.—*Trichadenia philippinensis* Merr. Transverse section. ×25.

Plate 2

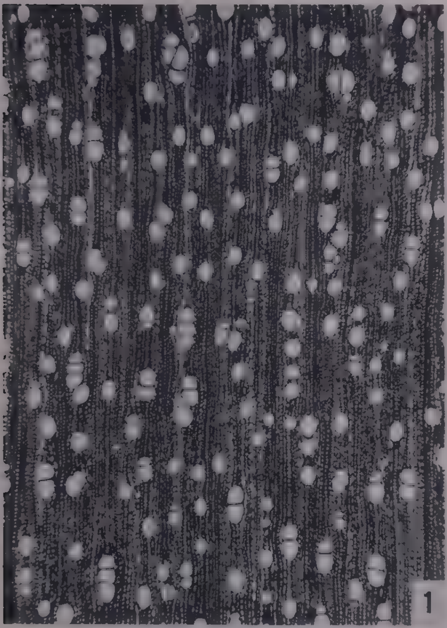
Fig. 1.—*Erythrospermum candidum* (Becc.) Becc. Transverse section. ×25.

Fig. 2.—*Erythrospermum candidum* (Becc.) Becc. Radial longitudinal section showing coarse gash-like vessel-ray pits, coarse intervessel pits, and multiple perforation plate. ×150.

Fig. 3.—*Casearia grewiifolia* Vent. Radial longitudinal section showing vessel-ray pits similar to the intervascular type, and crystals in rays. ×150.

Fig. 4.—*Homalium foetidum* (Roxb.) Benth. Tangential longitudinal section showing numerous heterogeneous rays and fine intervascular pitting. ×65.

WOOD ANATOMY OF FLACOURTIACEAE



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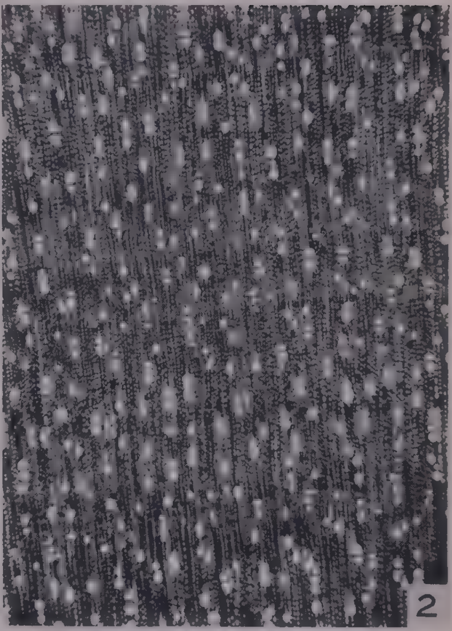

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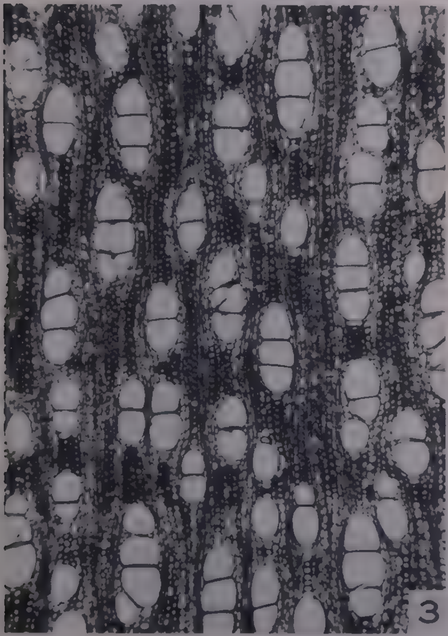

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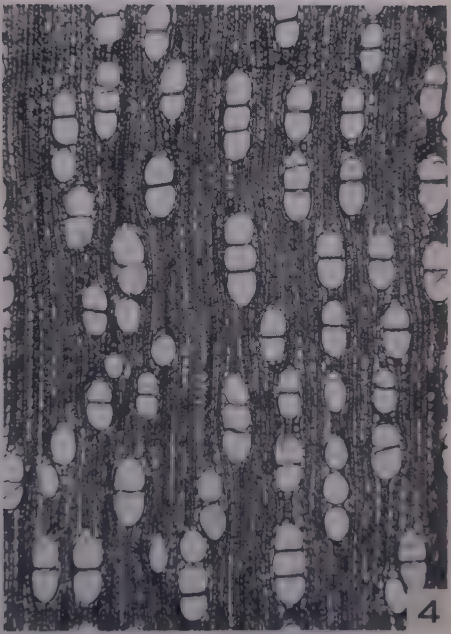

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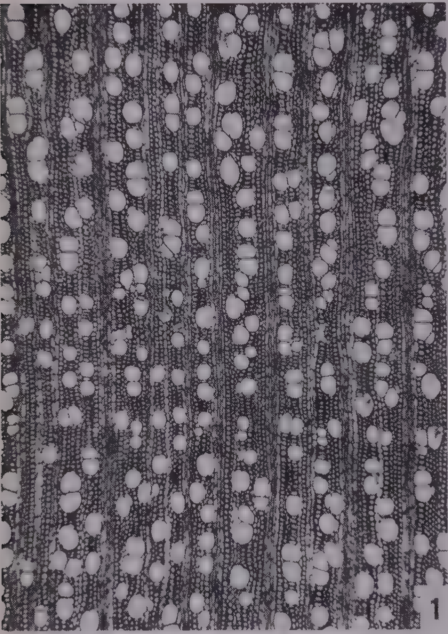
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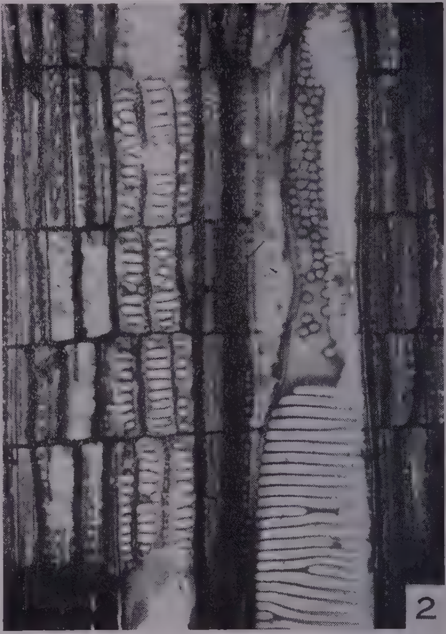
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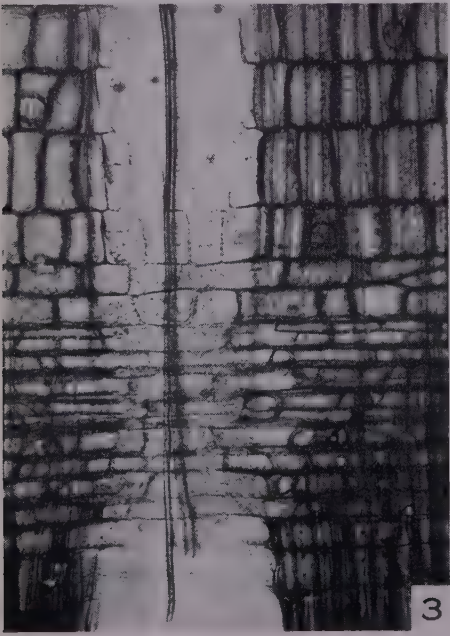
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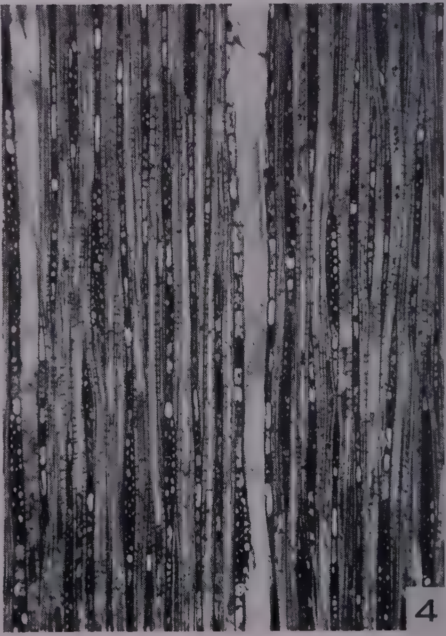
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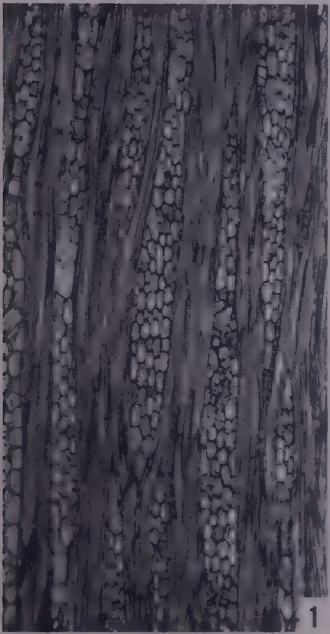
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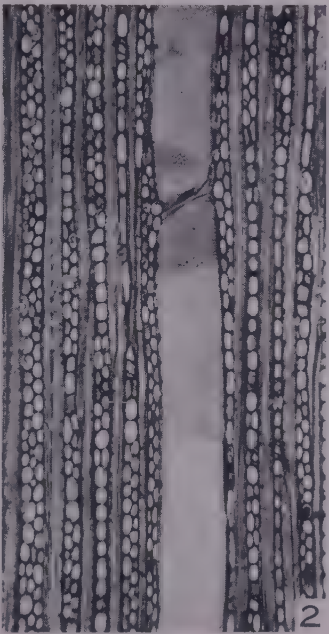
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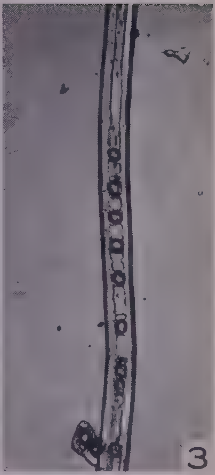
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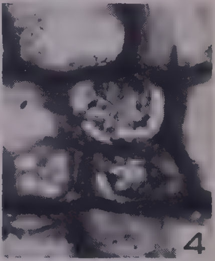
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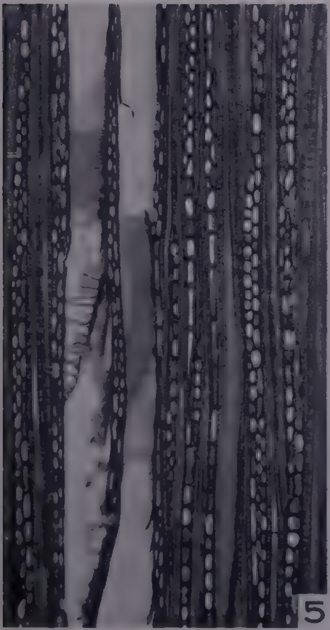
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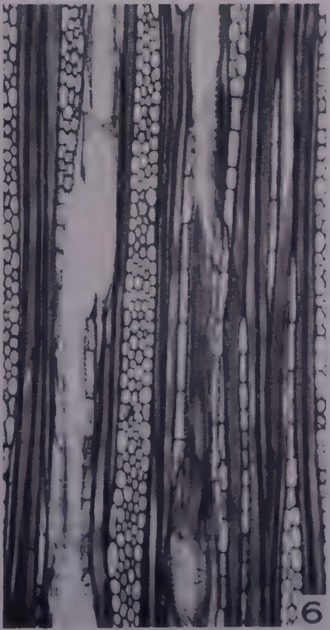
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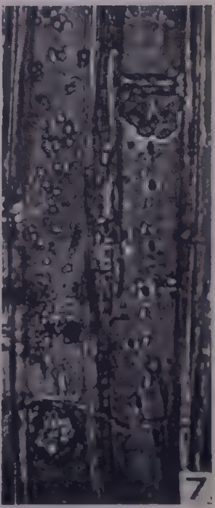
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PLATE 3

Fig. 1.—*Pangium edule* Reinw. Tangential longitudinal section. ×65.

Fig. 2.—*Trichadenia philippinensis* Merr. Tangential longitudinal section showing numerous rays and coarse intervascular pitting. ×65.

Fig. 3.—*Flacourtia inermis* Roxb. Macerated material showing chambered crystals in a septate fibre. ×150.

Fig. 4.—*Casearia fuliginosa* (Blanco) Blanco. Radial longitudinal section showing druses in unspecialized ray cells. ×400.

Fig. 5.—*Hydnocarpus kunstleri* (King) Warb. var. *tomentosa* (King) Sleum. Tangential longitudinal section showing numerous rays and coarse intervascular pitting. ×65.

Fig. 6.—*Erythrospermum candidum* (Becc.) Becc. Tangential longitudinal section showing uniseriate and multiseriate rays. ×65.

Fig. 7.—*Hydnocarpus sumatrana* (Miq.) Koord. Radial longitudinal section showing silica in septate fibres. ×400.

APPENDIX I

LIST OF GENERA AND SPECIES EXAMINED FOR COMPARISON WITH GENERA FROM THE SOUTH-WEST PACIFIC AREA

Species	Number of Samples	Country of Origin
Carpotroche amazonica Mart.	1	Brazil
Casearia arborea Urb.	1	Brazil
Casearia battiscombei R. E. Fries	2	Kenya
Casearia dolichophylla Standley	1	Mexico
Casearia javitensis H. B. and K.	1	Brazil
Casearia negrensis Eichl.	1	Brazil
Casearia sylvestris Sw.	1	Brazil
Casearia ulmifolia Cambess. (= *C. cambessedesii* Eichl.)	1	Brazil
Casearia (unassigned species)	1	Kenya
Gossypiospermum praecox (Gris.) P. Wilson	1	Cuba
Hasseltia sp.	1	Peru
Homalium tomentosum (Vent.) Benth.	1	India
Kiggelaria africana Linn.	1	South Africa
Kiggelaria (unassigned species)	1	South Africa
Laetia apetala Jacq.	1	Brazil
Laetia cupulata Spruce	1	Venezuela
Laetia procera (Poepp. and Endl.) Eichl.	1	British Guiana
	1	Surinam
	1	Brazil
Laetia thamnia L.	1	Mexico
Lindackeria maynensis Poepp. and Endl. (=*Oncoba maynensis* Poepp. and Endl.)	1	Brazil
Ryania chocoensis Triana and Planch.	2	Columbia, U.S.A.
Ryania pyrifera (L. C. Rich.) Uitt and Sleum.	1	Brazil
Scolopia mundtii Warb.	1	South Africa
Scolopia zeyheri Szyszyl. (includes *S. zeyheri* Warb.)	1	South Africa
Scottellia coriacea A. Cheval	1	Nigeria
Xylosma hemsleyana Standley	1	Mexico
Zuelania roussoviae Pittier	1	Mexico

THE INHERITANCE OF WOOD AND BARK CHARACTERS IN *EUCALYPTUS*

By L. D. Pryor,* M. Margaret Chattaway,† and N. H. Kloot†

[*Manuscript received March* 28, 1956]

Summary

Hybrids from segregating hybrid swarms have been examined in relation to the parents. Two series of hybrids were chosen, one derived from the combination *E. robertsoni* × *E. rossii*, of the group Renantherae, and the other from *E. elaeophora* × *E. maculosa* of the group Macrantherae-Normales. The hybrids and parents were assessed according to various physical and mechanical properties of the wood, features of bark structure, field characters, and measurements of characters in the progeny raised from each.

The properties of the hybrids were found to be either not significantly different from those of either parent or intermediate between those of the two parents. The degree to which they approached either parent in the various phenotypic characters examined was found, in the few cases where data were adequate, to be correlated closely with the genotype and likewise with its position in the range between the two parents. The graded sequence of variation in the characters of the different individuals in the hybrid combinations suggests those characters examined are, in general, under multiple factor control.

It is likely that most *Eucalyptus* hybrids are intermediate as a rule in their characters between the parents, and this applies to wood and bark characters as well as general morphological features.

I. Introduction

It is essential to know the mode of inheritance of wood characters in *Eucalyptus* to apply efficiently the results of genetic and breeding study to forestry practice. The length of time which it takes to produce a tree with well-developed true wood is so long that it prevents any quick, precise answer to the question. It is possible, however, to get an indication of the inheritance pattern for these characters by testing selected trees, already of adequate size, from hybrid swarms which occur naturally.

It is easy to find hybrids between some pairs of species under natural conditions and there are places where apparent hybrid swarms between two such species arise and thrive. The method employed was to select, from an area where such a swarm of suitable combination had developed, a series of trees within the swarm, each of which shows in a different degree, according to an estimate at sight, some inheritance from each of the two species. At the same time a number of trees was selected from what appeared at sight to be genetically pure stands of each of the parent species from the same general locality. From these trees wood and bark samples were taken, also a hand specimen and seed. From the seed progeny was raised. In each case the aim was to raise 50 plants. However, in most cases some were lost.

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† Division of Forest Products, C.S.I.R.O., South Melbourne.

Two species combinations were chosen: *E. rossii* × *E. robertsoni** and *E. maculosa* × *E. elaeophora*. Most of the trees sampled in the *E. rossii* and *E. robertsoni* swarm and the parent stands were about 40 years old with a D.B.H. between 12 and 15 in. A 6-ft butt log was cut for timber tests, suitably labelled, and the ends painted to minimize cracking. The material was similar from *E. maculosa* × *E. elaeophora* but the trees were probably somewhat younger and sampling was confined to 2-ft butt logs.

II. Evaluation of the Progeny Test

The only information about the genetic make-up of each individual is that which can be derived from a study of its progeny, since nothing is known of its pedigree. Seed collected in this way is open-pollinated and only the female parent is known with certainty. Such seed may be the result of selfing, or outcrossing to other hybrids, or backcrossing to either parental species. If it is crossed to another hybrid it is quite likely that any two such individuals involved in the crossing would differ very considerably from one another as they are likely to be segregates in the hybrid swarm, each with a different gene complement.

The common breeding system of *Eucalyptus* is not yet certainly known. Krug and Silveira Alves (1949), as a result of experiments with some *Eucalyptus* species planted in Brazil, concluded that the few species they examined were self-incompatible and that exclusive outcrossing was the rule. It is far from certain, however, that this is generally the case or that their result may not have depended in a large measure on the experimental technique. In some 20 species and some hundreds of individuals examined in the Australian Capital Territory it has been found that, with the exception of only one tree in only one species (*E. bicostata*), which is apparently self-incompatible, all species and individuals within those species are self-fertile. Of course, the fact that interspecific hybrids are found means that some outcrossing occurs. In any given species and locality the uncertainty is as to what percentage of outcrossing is common.

It is obvious from the variability which is encountered in *Eucalyptus* populations that the frequency of outcrossing is sufficiently high to maintain considerable genetic diversity.

Interpretation is further hampered by the fact that no known F_2 generation has yet been reported in *Eucalyptus*. A few F_1's have been synthesized (Brett 1949; Barber, personal communication 1952; Pryor 1954), and something is known of the expression of various characters in the F_1 generation. Most of them are a blend of those of each parent. This suggests that there is no dominance expressed as far as these characters are concerned. This is frequently the case with morphological characters in many woody plants (Stebbins 1950). In addition, numerous progenies which have been raised from supposedly hybrid individuals occurring naturally show marked segregation in many characters, and through each progeny there are frequently finely graded series for characters which have been examined. This suggests that in many of them there is multiple factor control and no dominance. Clifford's (1954) examination of a suspected swarm reveals a similar pattern. But, while this situation is by far the most common encountered, already some likely exceptions are known.

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* Nomenclature as in Blakely (1955).

The experimental material available, therefore, permits examination of the relationship between the phenotype of the individual tree, an assessment of its genotype from open-pollinated progeny, a measure of physical characters of the wood, and assessments based on bark and wood anatomy.

III. The Experimental Material

The two hybrid swarms chosen for study were, as mentioned in Section I, firstly between *E. rossii* and *E. robertsoni* and secondly between *E. maculosa* and *E. elaeophora*. The first pair of species belongs to the group Renantherae and the second pair to the Macrantherae-Normales. The selection of the pairs was determined mainly by the need to secure a combination between parents which in themselves have characters contrasting substantially with each other, particularly in the wood, bark, and juvenile leaves. There had also to be an adequate number of hybrid trees which could be felled and sampled. The *E. rossii* × *E. robertsoni* material was cut in November 1952, the *E. maculosa* × *E. elaeophora* in March 1954. The aim in each case was to select 10 trees of each parent, apparently genetically pure but growing within the same general locality, and 10 trees within the hybrid swarm, each combining in a different degree characters derived from each parent. The object was to raise 50 plants in every progeny from the separate trees and this resulted generally in about 35 surviving, although in some cases the progenies were smaller.

(*a*) *The* E. rossii × E. robertsoni *Hybrid Swarm*

This swarm was at Hall's Block in the Cotter Valley, A.C.T. It was found in a physiographic position which is frequently associated with the development of such hybrid combinations. *E. robertsoni* is normally a species found on sites of rather high quality which have some topographic shelter. *E. rossii* occurs on shallow soils and exposed north-west aspects. Although the two species are generally well separated in space, in some circumstances, owing to physiographic configuration, the two habitats are brought quite close together. The two species occur as the co-dominants in stands with other *Eucalyptus* species belonging to the Macrantherae-Normales but with which they apparently do not interbreed and these can therefore be disregarded for the present purpose.

Species which can interbreed occur as a rule in distinct ecological situations, and the areas occupied by the species meet along a quite sharp boundary according to the pattern previously described (Pryor 1953*b*). In this particular case the species in the region which can presumably interbreed were *E. rossii*, *E. robertsoni*, *E. macrorrhyncha*, *E. dives*, and *E. fastigata*. *E. rossii* was surrounded, according to the ecological situation, by *E. macrorrhyncha*, *E. dives*, and *E. robertsoni* within a distance of about 400 yd. *E. robertsoni* extended, however, a considerable distance before it reached a boundary some 2 miles distant with *E. fastigata* with which it is known to interbreed. Over a zone of some 100 yd between *E. rossii* and *E.*

robertsoni there were many trees intermediate in their phenotype in different degrees between the two parents.

The two species are quite distinct in their external morphology. *E. rossii* is known as "scribbly gum". It is smooth-barked and has dull, grey-green, rather thick leaves and hemispherical fruit with a slender pedicel and a flat rim (Fig. 1, Nos. 92–99). The juvenile leaves become alternate and petiolate after about the eighth pair (Plate 1, Fig. 1). On the other hand, *E. robertsoni*, called "narrow-leaved peppermint", has a rough bark which extends to the smaller branches, a rather bright, bluish green, thin leaf, and somewhat truncate-spherical fruits with a short, relatively thick pedicel (Fig. 1, Nos. 62, 64, 66, 67, 69, 70). The juvenile leaves are opposite for many pairs beyond the eighth and are sessile (Plate 1, Fig. 2). The internodes between the juvenile leaves are generally warty-glandular, especially in the earlier stages. The timber of *E. rossii* is generally somewhat superior in mechanical qualities to that of *E. robertsoni*.

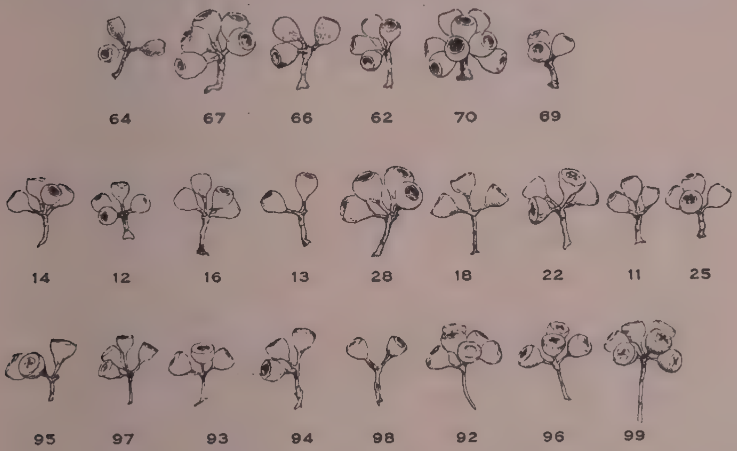

Fig. 1.—Nos. 62, 64, 66, 67, 69, 70, fruits of *E. robertsoni*, showing the range for the parent material. Nos. 92–99, *E. rossii*. Nos. 11–14, 16, 18, 22, 25, 28, hybrid. It will be noted in the hybrid range, particularly in the slender pedicel, that some of the combinations closely approach *E. rossii*, for example, Nos. 18, 22, and 16, whereas in this character and in fruit shape others approach *E. robertsoni*, for example, Nos. 12 and 25.

The supposedly hybrid individuals selected in the field were rated by eye on a ten-partite scale to show the apparent contribution from either parent species. This gave a subjective summation of all the characters normally used in identification of the species, in particular the general appearance and habit of the tree, the bark, leaves, fruits, and buds. The assessment is set out in Table 1. It will be noted in connexion with Nos. 67 and 70, which are in the group intended to represent pure *E. robertsoni*, that these were rated as 9–1 instead of 10–0. This was because, although when selected for sampling they were reckoned to be characteristic of the pure species, a closer examination of the hand specimen after cutting raised some doubt about their make-up and this was expressed by the 9–1 rating instead of 10–0.

TABLE 1

ASSESSMENT OF E. ROSSII, E. ROBERTSONI, AND THEIR HYBRIDS

Species	Tree No.	No. of Plants	Field Assessment		Progeny Assessment		Bark Assessment		Remarks
			E. robertsoni	*E. rossii*	*E. robertsoni*	*E. rossii*	*E. robertsoni*	*E. rossii*	
E. rossii	91	30	0	10	0	10			
	92	2	0	10	0	10			Very small progeny
	93	30	0	10	0	10			Some *macrorrhyncha* inheritance in 1 plant; some *robertsoni* in 1 plant
	94	29	0	10	0	10			
	95	33	0	10	0	10			Definite *macrorrhyncha* in 1 plant; very slight signs of *macrorryhncha* characters in 2 plants; very slight signs of *robertsoni* in 1 plant
	96	12	0	10	0	10			
	97	13	0	10	0	10			Slight signs of *macrorrhyncha* in 1 plant
	99	34	0	10	0	10			Slight *macrorrhyncha* in 1 plant; definite *fastigata* in 1 plant
	98	36	0	10	2	8			Definite appearance of *fastigata* characters in 1 plant and also *robertsoni* in 1 plant
Hybrids	11	14	9	1	10	0	9	1	Slight signs of *rossii* in 1 plant
	25	28	8	2	9	1	8	2	Definite *fastigata* characters as well as *rossii* and *robertsoni*
	12	33	7	3	7	3	7	3	Definite *macrorrhyncha* characters in 2 plants; *fastigata* in 1 plant
	28	19	6	4	5	5	9	1	
	13	34	5	5	9	1	4	6	*Rossii* characters in 1 plant
	16	8	4	6	4	6	6	4	
	14	33	3	7	3	7	4	6	*Macrorrhyncha* characters in addition to *rossii-robertsoni* in 1 plant
	22	34	1	9	1	9	3	7	Definite *robertsoni* characters
	18	16	1	9	1	9	2	8	

TABLE 1 (*Continued*)

Species	Tree No.	No. of Plants	Field Assessment		Progeny Assessment		Bark Assessment		Remarks
			E. robertsoni	*E. rossii*	*E. robertsoni*	*E. rossii*	*E. robertsoni*	*E. rossii*	
E. robertsoni	62	21	10	0	10	0			
	64	39	10	0	10	0			
	66	20	10	0	10	0			
	68	28	10	0	10	0			Definite *fastigata* in 1 plant
	69	42	10	0	10	0			
	61	9	10	0	9	1			Definite signs of *rossii* in 2 plants
	65	3	10	0	8	2			Small progeny
	67*	37	9	1	10	0			
	70*	37	9	1	9	1			Definite *fastigata* in 2 plants

* When selected these trees were thought to be "pure" *E. robertsoni*. After felling, with a specimen in hand these appeared to be a hybrid component which led to the rating 9–1.

When the progenies were well grown and had about 15 pairs of leaves and therefore when the 10th pair of leaves was well developed, they were assessed. This was done by measuring the length of the petiole of the 10th pair of leaves which had developed after the cotyledons. This particular point was chosen arbitrarily because it gave a simple metrical index. At this stage the leaves of *E. rossii* seedlings had become distinctly petiolate and alternate, whereas those of *E. robertsoni* were still entirely sessile and opposite. There are obviously other differences, such as colour, twisting of the leaves, and "falcateness" and "wartiness" of interodes, but these are more difficult to measure and no attempt was made to use them. The range of variation in one progeny, characteristic of the material, is shown in Plate 2, Figure 1. Table 1 shows the assessment of the progeny made on this basis, rounded off to the nearest unit. It should be noted that in allotting the numbers of individuals in a single progeny in the different petiole length classes to either parental group the number in the 1-mm class was divided equally so that half was allotted to the *E. robertsoni* side and half to the *E. rossii* side. This was done because at the limits of measurement the very small amount of rudimentary petiole which connects the sessile leaf of *E. robertsoni* to the stem is less than ½ mm long. This somewhat arbitrary basis was used to separate a sessile from a petiolate leaf. Figure 2 shows histograms based on this assessment.

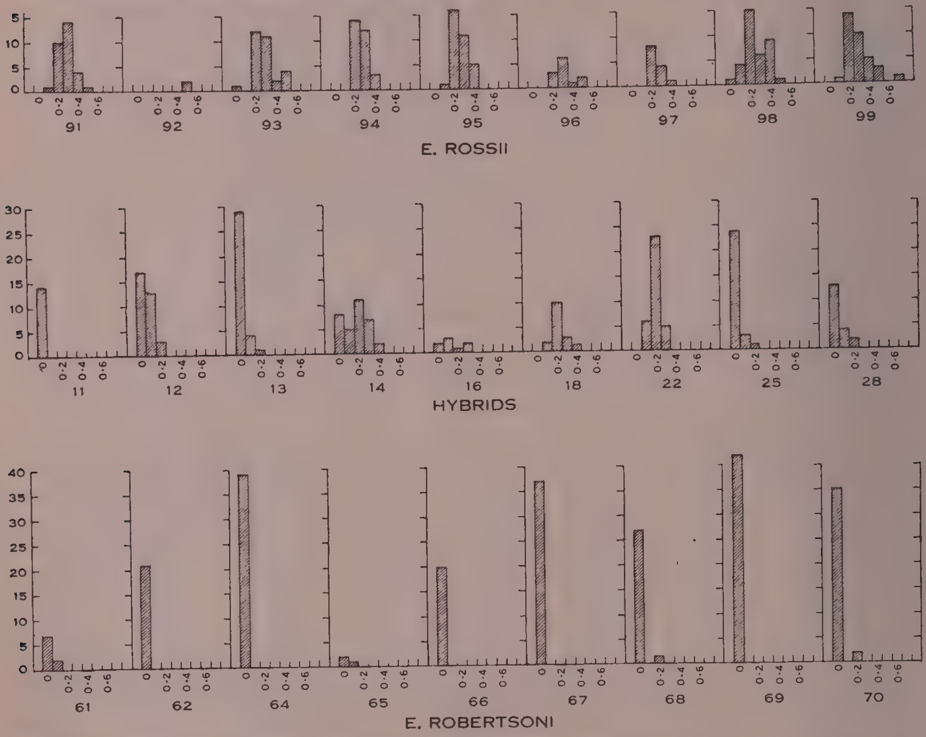

Fig. 2.—Histograms of petiole length of the 10th pair of leaves of *E. rossii*, *E. robertsoni*, an l the hybrids for comparison.

It will be seen that the original field assessment and the assessment made by measuring the progeny are quite closely related. The only major anomalies are in the *E. rossii* supposedly pure species, No. 98, in the *E. robertsoni*, No. 61, and in the hybrid range, No. 13. The variation, particularly No. 65 in the *E. robertsoni* series, may be disregarded because of the very few plants obtained. The correlation coefficient is 0·91, which is significant at $P<0{\cdot}001$. Additional variation of low frequency which occurred, apparently for a reason which was not suspected at the beginning of the trials, became apparent when the progenies were raised. These variations are noted in Table 1 by reference to the appearance of individuals displaying some of the characters of two other species, namely, *E. macrorrhyncha* and *E. fastigata*. The identification in the progeny of individuals with characters inherited from these species in hybrid combination is not difficult. Their occurrence warrants some discussion.

(*b*) "*Outliers*" *of* E. fastigata *and* E. macrorrhyncha *in Single Tree Progeny*

E. macrorrhyncha is easily identified in the juvenile state because of the presence of "stellate hairs" (strictly, bunches of hairs) which are highly distinctive for that species, and this is the only species within some 50 miles radius of the test site which has this character. Likewise, *E. fastigata* is readily identified by the leaf colour, texture, and shape, and there is no doubt that inheritance from this species has appeared in the progenies. The source of inheritance from these two species is still somewhat uncertain. There are two possibilities: either that they represent segregation from heterozygotes, mainly as the result of selfing, or that they are the result of direct outcrossing to the parental species or an F_2 or backcross segregate.

E. macrorrhyncha is quite close to the test site, a matter of 200 yd, but *E. fastigata* is some 2 miles from it. The occurrence of individuals with inheritance which can be definitely identified as *E. fastigata* is only about 0·7 per cent. of the total individuals raised in all progenies. This nevertheless represents a very high amount of outcrossing when, as in this case, the putative parents are separated by 2 miles. In the case of insect-pollinated species some data are available from Bateman's (1947) study of contamination of seed crops in insect-pollinated plants. By extrapolation from these data the percentage of outcrossing at 2 miles would be 0·019 per cent., or something less than 1/30th of the amount of the individuals noted with *E. fastigata* inheritance. While the measurements are few the difference is so great as to make it uncertain that the origin of these "outliers" is by outcrossing. In species that are wind-pollinated such a rate of outcrossing would be very high and for elm and poplar it would be of the order of only 0·0005 per cent. at 2 miles (Wright 1953).

Eucalyptus is certainly largely insect-pollinated and birds may play a part, but it is not in any degree wind-pollinated. This has been shown by many experiments by bagging controls with fabric through which pollen if wind-blown could easily pass, but no pollination takes place unless insects have access to the flowers.

In these circumstances in the above situation this frequency of *E. fastigata* hybrids, even though low, would imply a very high rate of outcrossing. If such were generally the case it would probably be difficult to obtain other than very mixed progeny from the two species *E. fastigata* and *E. robertsoni* when they are growing side by side, in those years when they flower heavily and simultaneously. In such cases, however, the seed obtained gives a progeny mainly like that of the parents and the amount of outcrossing is thereby indicated as low. It seems probable that the appearance of *E. fastigata* is the result of segregation of heterozygotes following selfing and that Nos. 68 and 70 in particular, which are otherwise pure *E. robertsoni*, probably carry some *E. fastigata* genes. If this is so it suggests that the hybridism may date to a much earlier period and may be connected with movements of species population boundaries associated with climatic oscillations. However, there must be further study of this to clarify the matter.

Another fact supports this tentative conclusion. Something is known of the shape of the juvenile leaves in F_1 hybrids between a few pairs of species and also the behaviour of petiole and "alternateness" of leaves in hybrid combination. It is found, if a logarithmic scale is used, that in several cases the leaf shape, measured by the ratio length : breadth, is intermediate between the parents (Barber, personal communication 1952; Pryor 1954). In the case of tree No. 70, however, the two plants with *E. fastigata* characters are considerably removed from the intermediate position in the direction of the *E. robertsoni* parent, which makes it quite unlikely also that they could result from direct outcrossing.

The position may well be similar with *E. macrorrhyncha* but it cannot be stated so clearly, as the evidence available from this test cannot be so easily interpreted. In the case of No. 25, the presence of three species in hybrid combination is recorded. This has already been described elsewhere (Pryor 1953*a*) and is by no means rare. The position is the same in Nos. 98 and 99. It may well be that there is some survival value in such combinations in hybrid swarms and that traces of the extraneous species tend to remain for this reason.

The occurrence of these "outliers" (Plate 2, Fig. 2) in the progenies, while of great theoretical interest, is much too low to affect the general analysis of the swarm. The fact is that trees which look hybrid in their external morphology produce progeny from open-pollinated flowers which generally indicate inheritance from either parent in the same proportion as does the external appearance of the tree. This supports the premise that most characters do not express dominance, or dominance is masked by multiple factor control, and in general that there is multiple factor control in character inheritance.

(*c*) *The* E. maculosa × E. elaeophora *Series*

The position with this series is essentially the same as for the previous set. *E. elaeophora* is at the limit of its range in the Australian Capital Territory and occurs as an isolated outlying stand on Mount Majura. Its place is taken further south by *E. cordieri* which is a closely related species but one which is apparently adapted to colder areas. *E. maculosa* is quite common, occupying somewhat exposed sites on Mount Majura and giving way to *E. stuartiana* on more sheltered sites. *E. rossii*, *E. dives*, *E. macrorrhyncha*, and *E. pauciflora* are also present but there is no evidence at all that they interbreed with the species being examined and they are disregarded in this case. *E. maculosa*, *E. elaeophora*, and *E. stuartiana* theoretically can interbreed. Sampling was done in the same way as for the previous material except that butt logs of 2 ft only were taken when it was found as the result of the mechanical tests on the first swarm that the extent of the tests could be considerably reduced. The trees appeared to be mostly about 30 years old and were about 9–18 in. D.B.H. In the case of the *E. elaeophora* parents, however, none of these could be found which were far removed from the hybrids; 100 yd was about the maximum. Progenies were raised and assessed on the breadth of the cotyledons. The cotyledons of *E. elaeophora* are about twice the width of those of *E. maculosa*, and this character gives a useful metrical assessment of the different progenies.

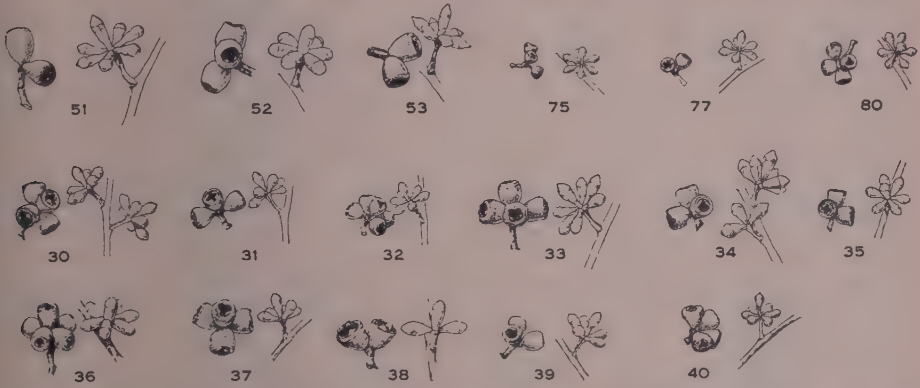

Fig. 3.—Nos. 51–53 showing buds and fruits of *E. elaeophora* covering the maximum variation in the whole of the centre; Nos. 75, 77, 80, *E. maculosa*, likewise showing the maximum range of variation; Nos. 30–40, hybrids between *E. elaeophora* and *E. maculosa*, showing, combined in different degrees, the characters from each parent. It will be noted in No. 38 that several inflorescences, one of which is shown, were three-flowered, and that the valves are distinctly exserted. Both of these characters are possibly derived from *E. viminalis* which may have hybridized at some relatively remote time in the past with the *E. elaeophora* and still be preserved in a slight degree in the segregates.

The two species are quite different. Of the two, *E. maculosa* is smooth-barked with narrow, rather light-textured leaves and small hemispherical pedicillate fruit with somewhat exserted valves. The buds are pedicillate and elliptical with the operculum about the length of the calyx tube (Fig. 3, Nos. 75, 77, 80). The juvenile leaves are alternate after two or three pairs and narrow-oblong to linear and petiolate. *E. elaeophora*, on the other hand, is a rough-barked tree with coarse, long, heavy leaves, sessile, barrel-shaped fruits with more or less included valves and with a thick, flattened peduncle. The buds are sessile and the operculum much shorter than the calyx tube (Fig. 3, Nos. 51–53). The juvenile leaves are orbicular, opposite, and sessile for a great many pairs. The wood of *E. maculosa* is pinkish brown and rather light, whereas that of *E. elaeophora* is yellow-brown and relatively heavy. The mechanical and physical properties of *E. elaeophora* are generally superior to those of *E. maculosa*. Incidentally, it is considered that the type of *E. westoni*, the type locality of which is near the area where the sampling was made, was an individual belonging to the hybrid swarm between these two species.

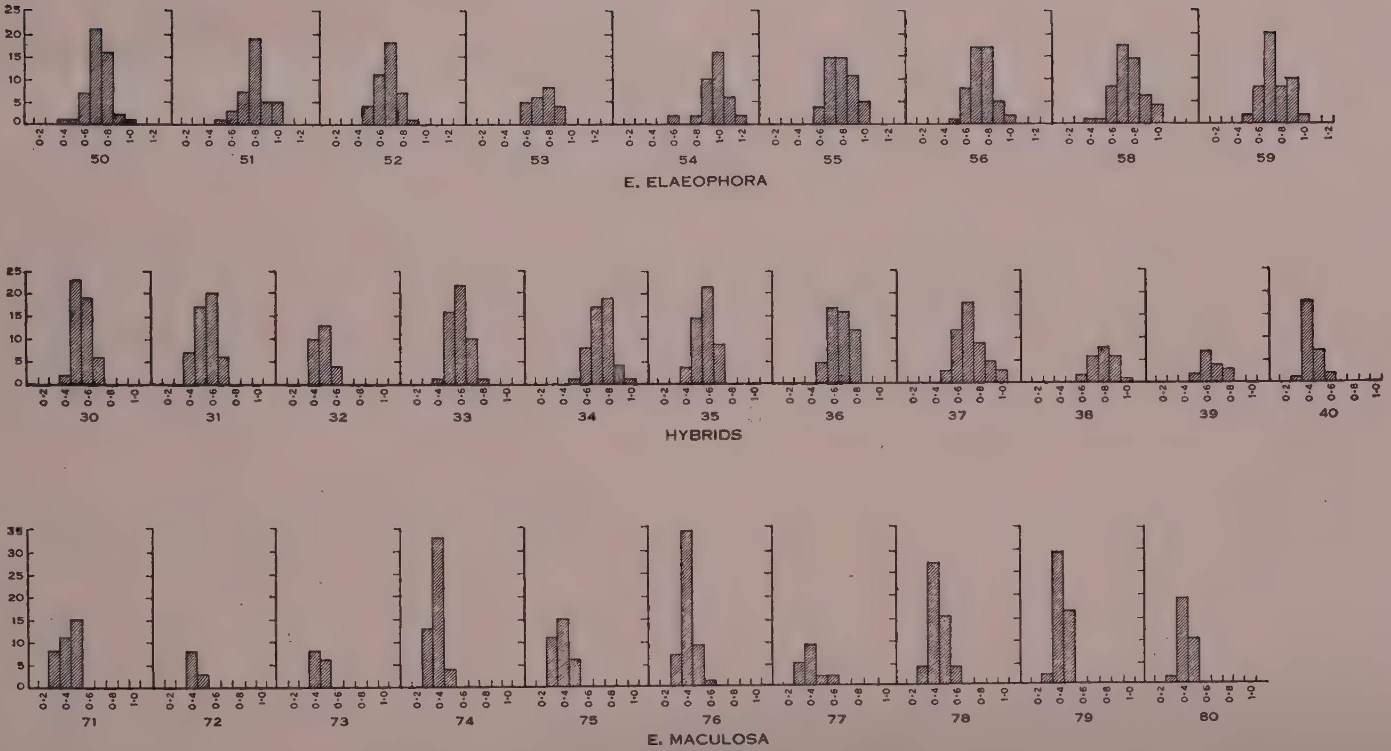

Fig. 4.—Histograms of cotyledon width of *E. elaeophora*, *E. maculosa*, and hybrids for comparison. It will be noted that the variance of the samples is greater in the *E. elaeophora* parents than in the *E. maculosa* parents. A logarithmic transformation would make the variances of the two parents more nearly equal and for some studies this procedure is desirable.

The results of assessing the progenies (shown by histogram, Fig. 4) were broadly similar to that of the previous combination except that in the correlation between the preliminary field assessment and the progeny assessment there were marked anomalies in three individuals, Nos. 31, 38, and 39 of the hybrids (Table 2). In

TABLE 2

ASSESSMENT OF E. ELAEOPHORA, E. MACULOSA, AND THEIR HYBRIDS

Tree No.	No. of Plants	Field Assessment		Progeny Assessment		Bark Assessment	
		E. maculosa	*E. elaeophora*	*E. maculosa*	*E. elaeophora*	*E. maculosa*	*E. elaeophora*
				E. elaeophora			
51	40	0	10	0	10	0	10
54	38	0	10	0	10	0	10
55	50	0	10	0	10	0	10
50	50	0	10	1	9	0	10
53	23	0	10	1	9	0	10
56	50	0	10	1	9	0	10
58	50	0	10	1	9	0	10
59	50	0	10	1	9	0	10
52	41	0	10	2	8	0	10
57	50	0	10	2	8	0	10
				Hybrids			
32	27	9	1	9	1	9	1
40	28	8	2	9	1	9	1
31	50	8	2	3	7	4	6
30	50	7	3	7	3	6	4
39	16	7	3	3	7	2	8
33	50	6	4	6	4	3	7
35	50	5	5	6	4	7	3
38*	23	4	6	0	10	7	3
37	50	2	8	2	8	3	7
34	50	2	8	1	9	2	8
				E. maculosa			
71	34	10	0	10	0	10	0
72	11	10	0	10	0	10	0
73	14	10	0	10	0	10	0
74	50	10	0	10	0	10	0
75	32	10	0	10	0	10	0
76	50	10	0	10	0	10	0
77	18	10	0	10	0	10	0
78	50	10	0	10	0	10	0
79	47	10	0	10	0	10	0
80	30	10	0	10	0	10	0

* Probably some inheritance from *E. viminalis.*

the case of No. 38 it seems likely that the deviation may be due to some genetic influence from *E. viminalis* in the individual. *E. viminalis* does not now occur in the immediate locality and the inheritance may be derived in a manner comparable with that of the *E. fastigata* in the previous swarm. It will be noted in the case of the *E. elaeophora* parents that only three based on the cotyledon measurements, Nos. 51, 54, and 55, appear to be completely pure. While the small amount of evidence available discloses no difference in the cotyledons of F_1 hybrids, whether derived from one maternal parent or the reciprocal, the cotyledonary assessment made here has the weakness that reduction in the cotyledon size by other than genetic control cannot be detected and this may make the results less precise than those from measurement of length and breadth of the eighth leaf pair in the seedling.

IV. BARK ANATOMY

(*a*) E. robertsoni × E. rossii

(i) *The Parent Species.*—The bark of *E. robertsoni* is a typical peppermint, rough-barked and somewhat fissured. The chief internal features are the large parenchyma wedges which run down into the inner phloem and are the sites of the cracks and fissures which give the characteristic appearance to the peppermints. These wedges are formed by division of the central cells of the wedge, which retain their meristematic condition. The fibre bundles form a regular pattern in the phloem, with a very even appearance of the fibres in cross section and a small cross-sectional diameter (Plate 3, Fig. 1).

The bark of *E. rossii* differs markedly from the above. There is no dead rhytidome, the bark shedding down to the innermost periderm. The most distinctive features are the layer of radially elongated phelloderm cells (Chattaway 1953, 1955*b*) and the great variation in fibre diameter between the fibres of different bundles. Both these features can be seen on a cross section of the bark (Plate 3, Figs. 2 and 3). The tangential diameter of the largest fibres reaches approximately 50 μ, and the radial diameter of the radially elongated phelloderm cells reaches approximately 150 μ.

(ii) *The Hybrids.*—The result of the anatomical examination of the 10 hybrids is given in Table 1, together with their assessment on field characters and on progeny tests.

In trees 11, 12, 15, and 25, the agreement between the two assessments is absolute: in trees 13, 14, 18, and 19 it is very close, the bark structure showing in two cases a greater tendency towards the *E. rossii* parent and in two cases slightly more *E. robertsoni* features. In trees 17, 22, and 28 there is a greater discrepancy between the two assessments, the bark features of *E. robertsoni* in trees 17 and 28 and of *E. rossii* in tree 22 being more marked than the morphological assessment suggests. A comparison of the progeny assessment with anatomical assessment gives a correlation coefficient of 0·68, which is significant at $P<0{\cdot}05$ (Table 11). Details of the characters of both parents and hybrids are given in Table 3.

(*b*) E. maculosa × E. elaeophora

(i) *The Parent Species.*—The bark of *E. maculosa* is smooth, peeled down to the innermost periderm. The distinguishing features, which are in the outer portion of the phloem, can be seen best on a cross section. They are a layer of radially elongated phelloderm cells (Chattaway 1953, 1955*b*), small, inconspicuous parenchyma wedges in the outer phloem, and numerous scattered oil glands which are not closely associated with the wedges (Chattaway 1955*a*). The fibres are in moderately conspicuous bundles, and the tangential diameter of the largest fibres reaches approximately 46 μ with an average of 41 μ (Plate 3, Fig. 4).

Table 3

BARK CHARACTERISTICS OF E. ROBERTSONI, E. ROSSII, AND THEIR HYBRIDS

Tree No.	Bark Assessment *E. robertsoni* : *E. rossii*	Bark Type	Parenchyma Wedges	Radially Elongated Phelloderm		Approx. Tang. Fibre Diameter of Largest Fibres (μ)
				Present	Rad. Cell Length (μ)	
			E. robertsoni			
61	10 : 0	Rough	Small	—	—	23
65	10 : 0	Rough	Large	—	—	20
69	9 : 1	Rough	Mod. large	—	—	45*
			Hybrid			
11	9 : 1	Rough	Large	—	—	30
25	8 : 2	Rough	Large	—	—	23
12	7 : 3	Rough	Large	—	—	38
28	9 : 1	Rough	Large	—	—	20
13	4 : 6	Smooth	Small	+	95	38
16	6 : 4	Rough	Mod. large	+	76	34
14	4 : 6	Smooth	Large	+	114	38
22	3 : 7	Smooth	—	Traces	68	45
18	2 : 8	Smooth	—	+	114	53
17	9 : 1	Rough	Mod. large	—	—	22
19	6 : 4	Rough	Mod. large	—	—	38
15	5 : 5	Smooth	Small	Traces	57	26
			E. rossii			
93	0 : 10	Smooth	Small	+	152	48
91	0 : 10	Smooth	—	+	190	42

* The fibre diameter of tree 69 (*E. robertsoni*) is unusually high for the species, which generally averages about 20–25 μ. Both the large diameter of the fibres and their appearance on cross section suggests the pattern of *E. rossii*, and this tree is assessed as 9 : 1, instead of 10 : 0, as it is suspected of being slightly divergent from the usual type.

Of 10 samples of *E. maculosa* examined for this investigation 3 varied slightly from the above type, in 1 the oil glands were fewer than usual, and in 2 others the radially elongated cells were less well developed. The parenchyma wedges were always small and inconspicuous.

TABLE 4

BARK CHARACTERISTICS OF E. MACULOSA, E. ELAEOPHORA, AND THEIR HYBRIDS

Tree No.	Bark Assessment *E. maculosa* : *E. elaeophora*	Bark Type	Parenchyma Wedges	Oil Glands	Radially Elongated Phelloderm		Approx. Tang. Fibre Diameter of Largest Fibres (μ)
					Present	Rad. Cell Length (μ)	
			E. maculosa				
71	10 : 0	Smooth	V. small	+	+	115	38
72	10 : 0	Smooth	Small	+	+	120	38
73	10 : 0	Smooth	V. small	+	+	123	38
74	10 : 0	Smooth	V. small	+	+	123	42
75	10 : 0	Smooth	V. small	+	+	95	40
76	10 : 0	Smooth	V. small	V. few	+	95	35
77	10 : 0	Smooth	V. small	++	+	114	38
78	10 : 0	Smooth	V. small	++	Traces	70	46
79	10 : 0	Smooth	V. small	+	Traces	57	46
80	10 : 0	Smooth	Small	+	+	95	45
			Hybrids				
32	9 : 1	Smooth	V. small	++	+	123	40
40	9 : 1	Smooth	V. small	++	+	114	55
31	4 : 6	Smooth	Mod. large	+	–		27
30	6 : 4	Smooth	Mod. large	+	Traces	57	30
39	3 : 7	Smooth	V. small	V. few	–		28
33	3 : 7	Smooth	Small	+	–		27
35	7 : 3	Smooth	Small	+	Traces	75	25
38	7 : 3	Smooth	Small	Few	+	75	30
37	3 : 7	Rough	Mod. large	++	–		25
34	2 : 8	Rough	Mod. large	+	–		20
36	1 : 9	Rough	Mod. large	Few	–		25
			E. elaeophora				
51	0 : 10	Rough	Large	+	–		20
54	0 : 10	Rough	Mod. large	Few	–		27
55	0 : 10	Rough	Large	+	–		23
50	0 : 10	Rough	Mod. large	+	–		20
53	0 : 10	Rough	Mod. large	Few	–		27
56	1 : 9	Rough	Small	Few	–		20
58	0 : 10	Rough	Mod. large	V. few	–		20
59	0 : 10	Rough	Large	+	–		25
52	0 : 10	Rough	Mod. large	+	–		23
57	0 : 10	Rough	Mod. large	Few	–		25

E. elaeophora is a rough-barked species without radially elongated phelloderm cells and with wide parenchyma wedges in which the oil glands occur. The fibre bundles are usually smaller than in *E. maculosa* and the diameter of the individual fibres is less, the largest tangential diameter is up to 27 μ with an average of 25 μ

(Plate 3, Fig. 5). Of the 10 samples of *E. elaeophora* investigated one had unusually small parenchyma wedges.

(ii) *Hybrids.*—Ten hybrid trees were examined; their bark covered a complete range from a smooth bark resembling *E. maculosa* to a rough one resembling *E. elaeophora.* In microscopic structure five of the trees showed characters tending towards the *E. maculosa* parent and five towards the *E. elaeophora* parent. Details of the characters of both parents and hybrids are given in Table 4.

V. The Mechanical and Physical Properties of the Wood

There appears to be little, if any, information available on the mechanical or physical properties of the wood of hybrid trees in relation to those of the parent species. The potential importance of such information, however, is obvious.

The results of tests conducted on the hybrids of the two pairs of parent species are as follows.

(*a*) E. rossii *and* E. robertsoni

From the 6-ft butt logs of 10 trees of supposedly pure *E. rossii*, 10 trees of supposedly pure *E. robertsoni*, and 12 trees representing varying degrees of crossing between these parent species, sampled as described above, a range of standard mechanical test specimens (British Standards Institution 1938; American Society for Testing Materials 1948) was prepared and tested in both the dry and green condition. A summary of the results is given in Table 5.

Table 5

MECHANICAL PROPERTIES OF E. ROSSII, E. ROBERTSONI, AND THEIR HYBRIDS

For the purposes of this table, trees having less than 25 per cent. of the *E. robertsoni* characteristics have been classified as *E. rossii* and vice versa. The remainder having characteristics varying between 25/75 and 75/25 of the parents have been classified as hybrids.

Property	Mean of Tree Means					
	In Green Condition			12% Moisture Content		
	E. rossii	Hybrid	*E. robertsoni*	*E. rossii*	Hybrid	*E. robertsoni*
No. of trees*	12	7	13	12	7	13
Density—						
Basic (lb/cu. ft)	41·0	37·1	35·6			
Air-dry (lb/cu. ft)				55·8	49·1	46·0
Static bending—centre pt. loading						
Fibre stress at L.P.† (lb/sq. in.)	5400	5400	5520	4800	6600	7800
Modulus of rupture (lb/sq. in.)	9210	9510	9330	11630	14180	12940
Modulus of elasticity (10^6 lb/sq. in.)	1·240	1·290	1·460	1·610	1·590	1·640

* In many instances, the number of test values averaged was substantially smaller than the number of trees sampled through the culling of results of defective specimens.

† Limit of proportionality.

TABLE 5 (*Continued*)

Property	Mean of Tree Means					
	In Green Condition			12% Moisture Content		
	E. rossii	Hybrid	*E. robertsoni*	*E. rossii*	Hybrid	*E. robertsoni*
Compression parallel to grain						
8 by 2 by 2 in. specimen						
Stress at L.P. (lb/sq. in.)	3200	3300	3100	2700	4000	4100
Maximum crushing strength (lb/sq. in.)	4430	4210	4320	5950	7520	7560
Modulus of elasticity (10^6 lb/sq. in.)	1·910	1·410	1·550	1·200	1·790	1·840
2 by 2 by 2 in. specimen						
Maximum crushing strength (lb/sq. in.)	4350	4210	4310	7810	8690	8350
Compression perpendicular to grain						
6 by 2 by 2 in. specimen						
Stress at L.P.—						
Radial (lb/sq. in.)	1160	870	750	1280	1050	1140
Tangential (lb/sq. in.)	1220	920	770	1200	1040	1110
Stress at 0·1 in. comp.—						
Radial (lb./sq. in.)	2520	1900	1650	2730	2190	2100
Tangential (lb/sq. in.)	2480	1930	1600	3160	2330	2280
2 by 2 by 2 in. specimen						
Stress at L.P.						
Radial (lb/sq. in.)	820	580	490	870	570	710
Tangential (lb/sq. in.)	710	580	520	1170	850	780
Stress at 0·1 in. comp.—						
Radial (lb/sq. in.)	1450	960	820	1920	1300	1290
Tangential (lb/sq. in.)	1280	980	850	2080	1670	1410
Hardness						
Janka value—						
Radial (lb)	1395	1190	1040	1970	1590	1270
Tangential (lb)	1375	1240	1000	2165	1480	1200
End (lb)	1350	1295	1120	2070	1750	1505
Cleavage strength—						
Radial (lb/in.)	296	303	318	332	304	375
Tangential (lb/in.)	260	356	348	—	426	368
Toughness value—						
Radial (in. lb)	145	158	116	123	108	97
Tangential (in. lb)	161	159	110	83	141	108
Izod value—						
Radial (ft lb)	7·3	9·0	7·2	4·2	7·0	5·2
Tangential (ft lb)	7·7	8·8	8·1	3·6	8·4	5·9

On analysis of these results, it was found that, with the exception of density, compression strength perpendicular to grain, and hardness, which are usually highly correlated with one another, there was no significant difference between the properties of the parents and those of the hybrids. However, as the properties of *E. rossii* were in general higher than those of *E. robertsoni*, it was clear that inadequacy of the sample was mainly responsible for other differences between the two species and the hybrids proving to be statistically non-significant.

The logs were resampled to provide a comparatively large number (approximately 20) of 2 by 1 by 1 in. specimens from each log. The whole cross section of each log from pith to bark was fully represented in these specimens which were tested in the green condition, in compression parallel to the grain. Density determinations were also made. The results of these tests are summarized in Table 6.

TABLE 6

DENSITY AND COMPRESSION STRENGTH OF E. ROSSII, E. ROBERTSONI, AND THEIR HYBRIDS

Group		No. of Trees	Average Max. Crushing Strength (lb/sq. in.)	Average Basic Density (lb/cu. ft)
E. rossii (%)	*E. robertsoni* (%)			
0– 5	95–100	9	4820	33·2
6– 35	65– 94	6	5100	35·0
36– 64	36– 64	4	5080	35·9
65– 94	6– 35	4	5380	38·6
95–100	0– 5	9	5220	39·7

It was found on analysis that for maximum crushing strength the means of tree means for the five groups shown in Table 6 did not differ significantly. The density variation on the other hand was significant at $P < 0 \cdot 01$, the grouping accounting for 61 per cent. of the total variation in density. This grouping was based on the original field assessments of the hybrids.

With the later assessments based on progeny examination, the correlation between density and degree of hybridization was slightly improved, 66 per cent. of the variation being accounted for by degree of hybridization as assessed by progeny measurement. No significant correlation was found between the assessment and maximum crushing strength, the former accounting for only 10 per cent. of the variation in the latter.

Shrinkage tests were also made on material from the logs and the results are summarized in Table 7. *E. rossii* was shown to have a significantly higher shrinkage than *E. robertsoni* and generally speaking, the hybrids as a group with a shrinkage intermediate between those of the parents differed significantly from either parent.

(*b*) E. maculosa *and* E. elaeophora

On the experience gained with the *E. rossii* × *E. robertsoni* hybrids, it was decided to limit the testing of *E. maculosa* × *E. elaeophora* hybrids to the determination of density, maximum crushing strength, and shrinkage. The results of the shrinkage test are not yet available.

TABLE 7

SHRINKAGE DATA FOR E. ROSSII, E. ROBERTSONI, AND THEIR HYBRIDS

Shrinkage Treatment	Mean Shrinkage (%)			Significance of Differences Between Means		
	E. rossii	*E. robertsoni*	Hybrids†	*E. rossii* and *E. robertsoni*	*E. rossii* and Hybrids	*E. robertsoni* and Hybrids
Green to 12% moisture content						
Before reconditioning						
Radial	8·8	8·7	6·4	**	**	N.S.
Tangential	13·5	10·0	12·6	**	N.S.	*
After reconditioning						
Radial	4·1	2·9	3·0	**	**	N.S.
Tangential	6·4	5·1	5·9	**	*	**
Green to oven-dry						
Radial	6·3	4·9	5·0	**	**	N.S.
Tangential	9·4	8·2	8·9	**	N.S.	*

* $P<0{\cdot}05$. ** $P<0{\cdot}01$. N.S., not significant.

† "Hybrids" refers to all those originally labelled as such in the original field assessment.

From the small butt log sections of 10 trees of *E. maculosa*, 10 trees of *E. elaeophora*, and 11 trees of their hybrids, small specimens 2 by 2 by 1 in. were prepared and tested in a green condition and in a similar manner to the *E. rossii* × *E. robertsoni* specimens. The results are summarized in Table 8.

The correlation between density and degree of hybridization based on the progeny assessment was found to be slightly lower than for the first pair of species, the correlation coefficient being 0·75 compared with 0·82 obtained for *E. rossii* × *E. robertsoni*. However, the correlation between maximum crushing strength and degree of hybridity was found to be higher than that obtained for the hybrids of the other species, the correlation coefficient being 0·68 and significant at $P<0{\cdot}01$ probability level, the better relationship arising from the greater degree of correlation between crushing strength and density in the case of the *E. maculosa* × *E. elaeophora* specimens. For the latter, 68 per cent. of the variation in maximum crushing strength was attributable to variation in density whereas in the *E. rossii* × *E. robertsoni* combination only 47 per cent. of the strength variation could be accounted for by density variation.

(*c*) *Discussion*

The results obtained thus far with the two groups of parents and their hybrids are compatible with the hypothesis that the mechanical and physical properties of the hybrids are intermediate between those of the parent species. A much more extensive sampling than has hitherto been attempted would be necessary to establish whether or not the properties of the hybrids are linearly related to the degree of hybridity. Assuming a property variability (coefficient of variation) of 12½ per cent., which is quite normal for some strength properties, and a difference between two parent species in this property of 10 per cent., then an idea of the size of sample required for such an investigation may be gained. To show that a practically significant departure from linearity (±2½ per cent. or more) from the expected value of 1·05 per cent. for the hybrids was highly significant would require specimens from 170 trees of each parent species and 340 hybrid trees. Such a programme would be impracticable and it would appear that future investigations must, by restriction of the size of the sample, be limited to determining whether the properties of the hybrids fall between those of the parents or outside them.

TABLE 8

DENSITY AND COMPRESSION STRENGTH OF E. MACULOSA, E. ELAEOPHORA, AND THEIR HYBRIDS

Group		No. of Trees	Average Max. Crushing Strength (lb/sq. in.)	Average Basic Density (lb/cu. ft)
E. maculosa (%)	*E. elaeophora* (%)			
0– 5	95–100	3	5260	41·4
6– 35	65– 94	11	5490	44·4
36– 64	36– 64	2	5020	41·5
65– 94	6– 35	2	4820	39·8
95–100	0– 5	11	4540	37·2

VI. WOOD STRUCTURE

The essential characters of wood structure are closely similar in the two species *E. rossii* and *E. robertsoni*. The same is true of *E. maculosa* and *E. elaeophora*. It was found also that the anatomical characters in the first pair of species were so close that extensive measurements would certainly have been necessary to establish a metrical difference even if one did exist; this was considered unwarranted. In the case of *E. elaeophora* and *E. maculosa*, however, there were three characters which offered some promise. They were firstly the presence of crystal cells in the xylem parenchyma of the *E. maculosa* as compared with the absence of this in the *E. elaeophora*, secondly the triseriate rays in *E. elaeophora* and their absence in *E. maculosa*, and thirdly the fact that the tangential diameter of the vessels of *E. elaeophora* is substantially greater than that of *E. maculosa*.

The position with regard to the presence of crystal cells is set out in Table 9. It will be noted that as with the bark characters the hybrids as a group show themselves to be generally intermediate between the two parents, some being with and others without the character.

TABLE 9

OCCURRENCE OF CRYSTALS OF CALCIUM OXALATE

+ Present — Absent

Sample tree	*E. elaeophora*	32	40	31	30	39	33	35	38	37	34	36	*E. maculosa*
Crystals	Present in all samples	—	—	—	—	—	—	+	—	+	+	+	No crystals

In the case of tangential vessel diameter, the variance within each of the parents is too large to permit precise analysis from the rather limited data and on the available figures it can simply be said that the hybrids as a group are intermediate between the two parents. The results of these measurements are set out in Table 10.

TABLE 10

TANGENTIAL PORE DIAMETER

E. elaeophora		Hybrid		*E. maculosa*	
No.	Mean of 10 (mm)	No.	Mean of 10 (mm)	No.	Mean of 10 (mm)
50	1·37	32	1·48	71	1·25
51	1·57	40	1·29	72	1·40
52	1·44	31	1·28	73	1·24
53	1·78	30	1·51	74	1·25
54	1·45	39	1·32	75	1·31
55	1·44	33	1·34	76	1·37
56	1·30	35	1·34	77	1·35
57	1·56	38	1·60	78	1·24
58	1·55	37	1·40	79	1·37
59	1·30	34	1·39	80	1·34
		36	1·22		
Mean	1·48	Mean	1·38	Mean	1·31

It is safe to say, therefore, that, as with most of the other characters examined, wood structure in hybrid combination, at least in the case of the *E. maculosa-E. elaeophora* pair, is generally intermediate between the two parents, but to examine this relationship more closely would probably need extensive sampling comparable with that necessary to give more precision to the examination of the physical properties of the wood, and this is not justified at present.

VII. GENERAL DISCUSSION

The correlation shown in Table 11, in which the correlation coefficient is given, indicates significant and fairly close agreement between genetic make-up as assessed by the open-pollinated progeny obtained from an individual and its phenotype assessed in various ways, particularly by bark anatomy, physical characters of the wood, and external morphology (field assessment). Even though the progeny assessment has been made on only one character, in each case it is highly probable that the character chosen is determined by several genes and therefore expresses in a closely graduated sequence the inheritance in accordance with the multiple factor pattern. The field assessment and the bark anatomy assessment are both estimates of the phenotype made by a subjective summation of characters. From the data it is concluded that there is a close relationship between the genotype and phenotype in the hybrid combinations or, to put it differently, trees which look hybrid are found to have inheritance from the putative parents quite closely in the proportion that the phenotype implies.

TABLE 11

CORRELATION COEFFICIENTS BETWEEN PROGENY ASSESSMENT OF HYBRIDS AND ASSESSMENTS BASED ON OTHER CHARACTERS

	Field Assessment	Bark Anatomy	Timber Characters	
			Density	Max. Crushing Strength
E. robertsoni × *E. rossii* Progeny assessment	0·91***	0·68*	0·81**	0·32 N.S.
E. elaeophora × *E. maculosa* Progeny assessment	0·68*	0·64*	0·75**	0·68**

* $P<0{\cdot}05$. ** $P<0{\cdot}01$. *** $P<0{\cdot}001$. N.S., not significant.

While the data relating to the wood anatomy are rather scanty, it is likely that the same position exists there.

With regard to the physical and mechanical properties of the wood, no doubt these are determined by many characters of the wood which are at least under separate gene control and perhaps the result of action by several genes, and it is highly probable that there are multiple factors concerned in determining the inheritance of any particular mechanical or physical property of the wood. In the material examined it is clear that the wood characters of the hybrids in general are intermediate between those of the parents. While no firm generalization is permissible from the relatively limited material, much wider observations in the field of the more obvious characters of the wood of many hybrids accord with the same view.

There are some grounds for thinking, therefore, that in hybrids such as may be developed to improve *Eucalyptus* yields in the wide variety of places where they are now being used in plantations there is a good chance that the hybrid will be intermediate in its characters, and in particular in its wood characters, between the parents. A breeding programme might well be organized, in the first instance, with such expectation. Exceptions to this, of course, would be of the greatest importance. Perhaps the most outstanding example in all plants of the character possessed by a hybrid being outside the range covered by the two parents is that of hybrid vigour of growth, where greatly increased growth rates beyond those of either parent are found. Even in relation to this character, however, in most viable hybrids the growth is as a rule intermediate between that of the two parents, excluding those cases where the growth is much less than in either of the parents. By this analogy, therefore, it seems that cases might well occur, though perhaps infrequently, in which the physical properties of the wood are substantially greater or substantially less than those of either of the two parents. The discovery of either case would be of great importance, since one could lead to very marked improvement in yield while the other might result in the failure of a combination derived by breeding. Future work in this field might therefore well be directed to attempts to locate any such cases from the wide range of hybrid material available from natural stands in many parts of Australia. From the experience of the present trial, methods of sampling can now be developed to make the testing of such occurrences easier than in this study.

VIII. ACKNOWLEDGMENTS

The assistance of Mr. G. A. McIntyre in discussion on some of the statistical aspects is recorded with pleasure. Thanks are due also to Mr. O. Ruzicka for the figures, and to Mr. W. Pedersen for the photographs.

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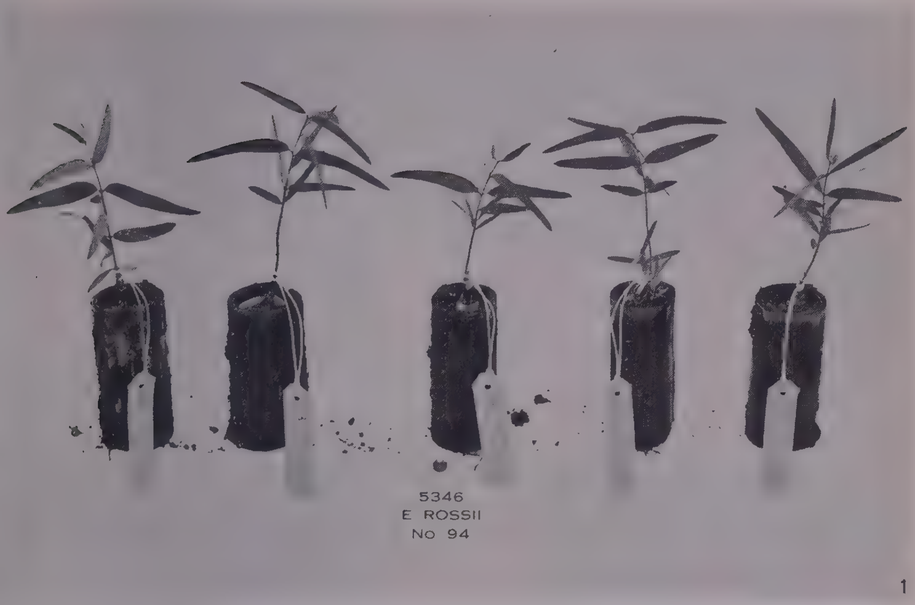
WOOD AND BARK CHARACTERS IN EUCALYPTUS



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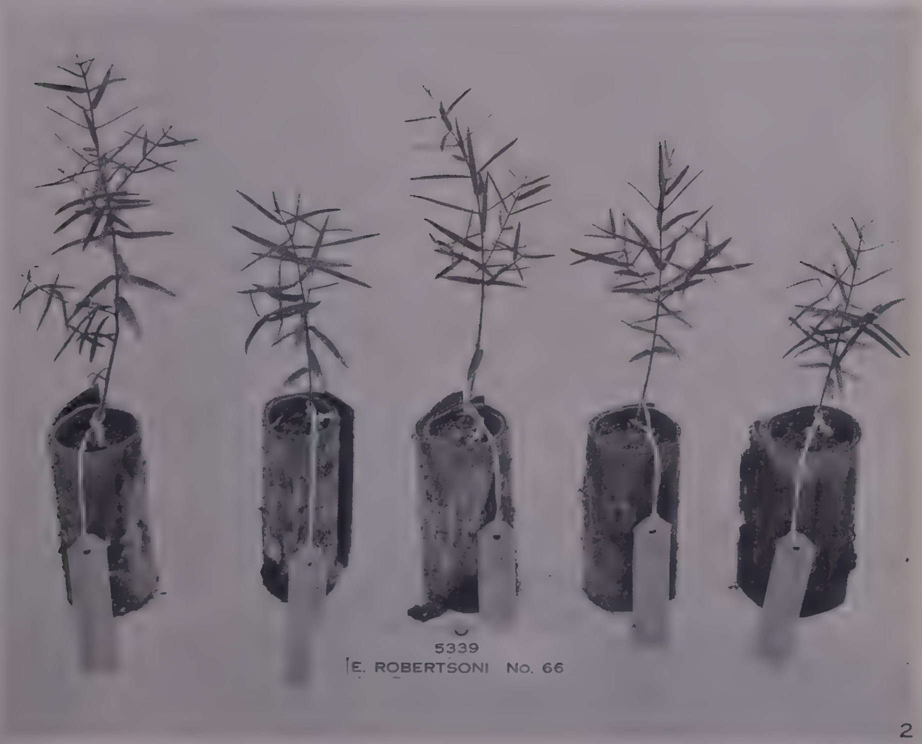

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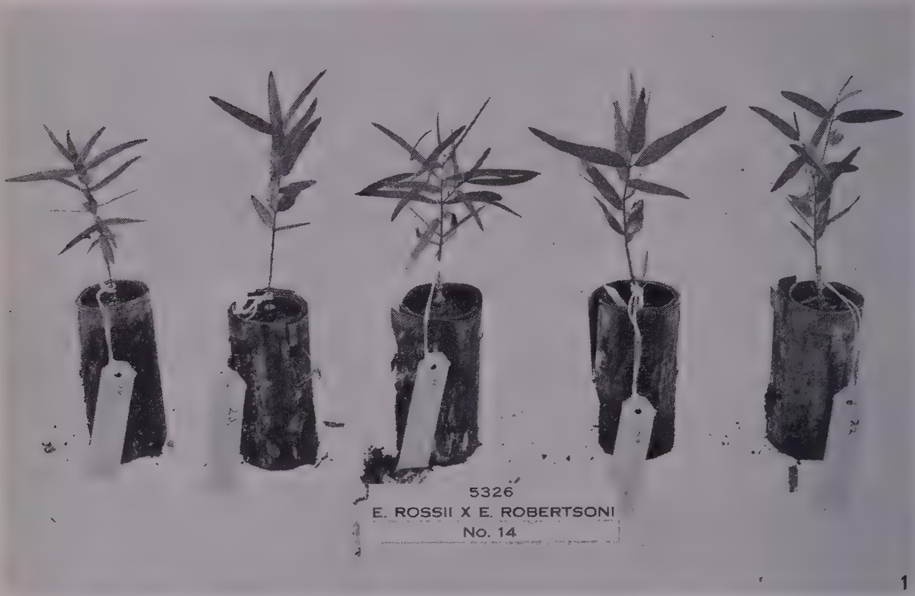
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No. 14

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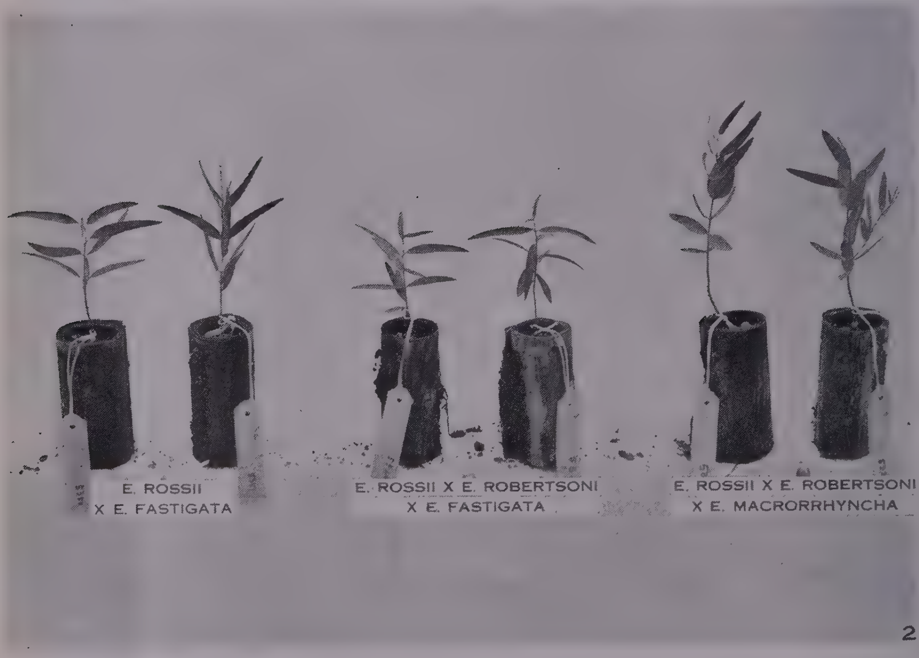
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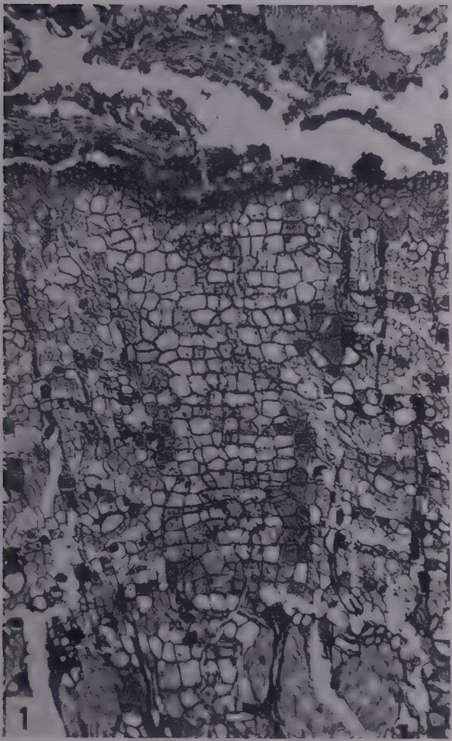
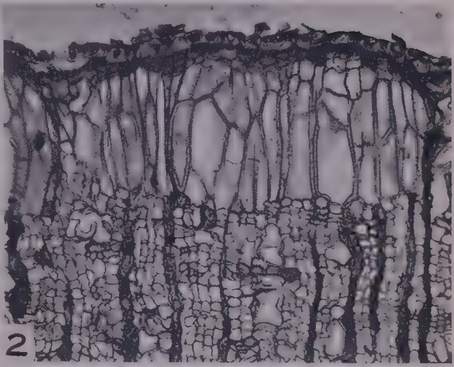
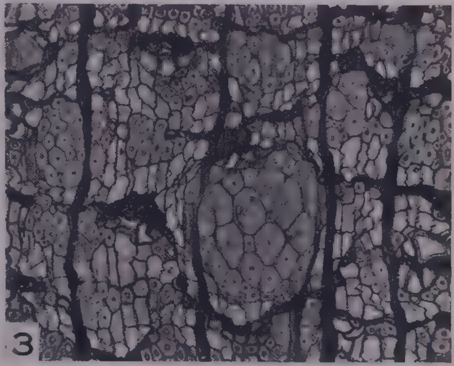
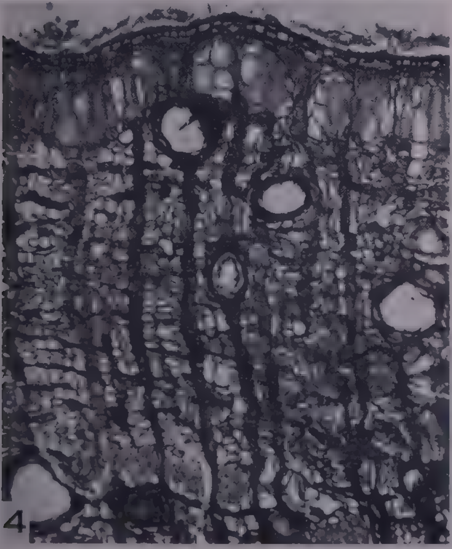
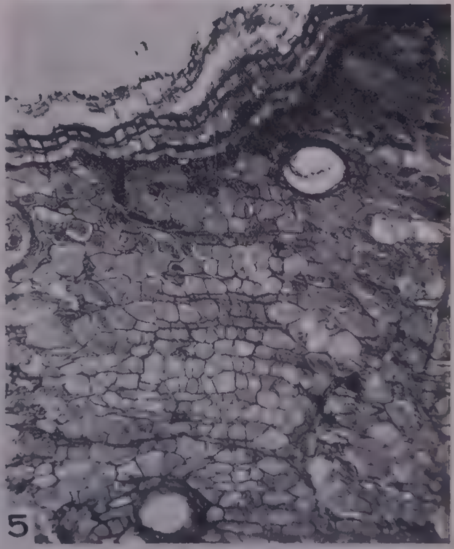
WOOD AND BARK CHARACTERS IN EUCALYPTUS











Explanation of Plates 1–3

Plate 1

Fig. 1.—The maximum degree of variation obtained in the progeny of apparently genetically pure *E. rossii.*

Fig. 2.—The maximum variation in the progeny of pure *E. robertsoni.*

Plate 2

Fig. 1.—Segregation in hybrid No. 14, *E. rossii* × *E. robertsoni*, showing on the right an individual almost identical with *E. rossii* and on the left one almost identical with *E. robertsoni*, with some intermediates.

Fig. 2.—"Outliers" of *E. rossii* × *E. fastigata* at left; *E. rossii* × *E. robertsoni* × *E. fastigata* centre, and *E. rossii* × *E. robertsoni* × *E. macrorrhyncha* at right.

Plate 3

Fig. 1.—*E. robertsoni*: cross section of outer phloem, showing wedge of parenchyma. ×65.

Fig. 2.—*E. rossii*: cross section of outer phloem, showing radially elongated phelloderm. ×65.

Fig. 3.—*E. rossii*: cross section of phloem showing bundle of large fibres. ×65.

Fig. 4.—*E. maculosa*: cross section of outer phloem showing radially elongated phelloderm and scattered oil glands. ×65.

Fig. 5.—*E. elaeophora*: cross section of outer phloem showing parenchyma wedge and oil glands. ×65.

TRILETE SPOROMORPHS FROM AUSTRALIAN PERMIAN SEDIMENTS

By B. E. Balme* and J. P. F. Hennelly*

[*Manuscript received April 23, 1956*]

Summary

This paper, in conjunction with two earlier publications by the same authors (Balme and Hennelly 1955, 1956), completes the taxonomic revision of a number of the common sporomorphs occurring in Australian Permian sediments. Twenty-six sporomorphs bearing triradiate tetrad scars are illustrated and described, the majority being assigned to existing genera of Palaeozoic fossil spores. Two new organ genera, *Tholosporites* n. spt. and *Bascanisporites* n. spt. have, however, been created to receive morphological categories differing from any previously described. A short discussion on the distributions and possible affinities of the sporomorphs treated is included.

I. Introduction

Sporomorphs of either simple or complex structure possessing a triradiate tetrad marking and lacking any other obvious germinal mechanism have a long geological history. They have been reported from Cambrian sediments in India and Europe by a number of authors (e.g. Darrah 1937; Naumova 1949; Jacob, Jacob, and Shrivastava 1953) although these interpretations are still the subject of some controversy (Hoffmeister and Staplin 1955). Their occurrence in Devonian beds is, however, well authenticated (Lang 1925; Arnold 1936; Naumova 1937) and, apart from a few monolete forms recently reported from the Upper Devonian of North America (Hoffmeister, Staplin, and Malloy 1955), all known Devonian spores are trilete. Spore floras of pre-Namurian Carboniferous sediments in Europe are basically similar to those of the Devonian (cf. Luber and Waltz 1938; Raistrick 1938; Knox 1948) and are, again, composed almost entirely of trilete forms some of which are comparatively complex structurally. In the Westphalian of Europe and the Pennsylvanian of North America, trilete spores, although they still dominate the assemblages, are accompanied by large numbers of sporomorphs of greater morphological complexity such as *Florinites*, *Schopfipollenites*, and *Illinites*, and, although they occur frequently in Mesozoic and Tertiary sediments, trilete forms become less important microfloral elements after the end of the Carboniferous.

Little information exists on the spores occurring in pre-Sakmarian deposits in Gondwanaland, but recent examination of the plant microfossils from black shales of probable Westphalian age from the Kimberley District of Western Australia have shown that simple and rather indistinctive trilete types predominate in the assemblages. The Gondwanaland Permian spore assemblages on the other hand show a great diversity of types, and trilete forms, although still plentiful, are matched in abundance by pollens and pre-pollens, and by bilaterally symmetrical spores possessing monolete tetrad scars. Some of the trilete spores occurring in Indian and Australian Permian sediments have been described by earlier authors

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* Coal Research Section, C.S.I.R.O., Sydney.

(e.g. Dulhunty 1945; Virkki 1945; de Jersey 1946), and while a few of these forms are simple and indistinctive others are well characterized and known to be of stratigraphical importance (cf. Dulhunty 1946; Balme 1952).

II. Affinities of Trilete Sporomorphs

Trilete spores are widespread among the lower plant groups of the present day. They are almost universal in the Lycopodiaceae and Selaginellaceae (Knox 1950), and many bryophytes also produce radially symmetrical trilete spores, some of them of complex structure and ornament (Knox 1939). Many present-day fern species are known to possess trilete spores and there seems little doubt that the majority of trilete forms occurring in Upper Cretaceous and Tertiary sediments have filicalean affinities. It is, however, dangerous to extrapolate from analogy into the early Mesozoic and Palaeozoic, and little can be decided as to the affinities of Permian types. Few fossil spores have been related with certainty to their parent plants, although present evidence suggests that members of the Lepidodendraceae and Sigillariaceae all possessed trilete spores. Other ancient pteridophyte groups members of which are known to have produced trilete spores include the Calamitaceae (Hartung 1933), Noeggerathiales (Nemejc 1935), and Sphenophyllineae (Knox 1938), while the spores of *Dactylotheca plumosa* Artis and *Senftenbergia ophiodermatica* Goppert (two of the few Palaeozoic fern species from which spores have been described) are heavily ornamented and bear a clear triradiate marking (Radforth 1938).

Trilete spores have also been found in presumably non-pteridophyte fructifications. The pollen grains of *Crossotheca hughesiana* and *C. honingshausi* are, from Kidston's original illustrations (Kidston 1906), indistinguishable from the trilete spores of pteridophytes, although Florin (1937) has suggested that they may also have been equipped with a single distal furrow. The pollen grains of *Renaultia gracilis* and *Paracalathiops stachei* on the other hand are clearly functionally trilete (Florin 1937; Remy 1954), and if the systematic position of these two plants is accepted the possibility that isolated fossil trilete grains belong to pteridosperms cannot be excluded. Similarly the pollen grains of *Cycadocephalus sewardii* have a marked pteridophyte aspect (Nathorst 1909), and again assuming that the assignation of this fossil to the Bennettitales is correct some late Palaeozoic and Mesozoic trilete sporomorphs may have derived from Cycadophytes.

While it would be reasonable to assume, therefore, that the majority of the sporomorphs described in this account derive from bryophytes or pteridophytes, it is impossible to assign affinities to any of the individual sporomorphs. Some may be pteridospermic (those classified under *Nuskoisporites*, for example, bear a superficial resemblance to the pollen grains of *Paracalathiops* and *Thuringia*) while others, such as the *Tholosporites* group, do not resemble the spores of any known living or fossil plant.

III. Classification

The presence or absence of a presumably functional triradiate tetrad scar was one of the earliest classificatory criteria applied by students of fossil spores. Reinsch (1884) first proposed the name *Triletes* as a general category for all spores marked in this way, although it is apparent that he had no clear idea as to the nature of the fossils which he illustrated. *Triletes* was used by Bennie and Kidston (1886), in a more limited sense, as a form genus for megaspores of lycopodiaceous aspect. Schopf (1938), who amended the original definition of Reinsch, formally adopted this usage which has been observed by most other authors of papers on Palaeozoic megaspores. Recently, however, Potonié and Kremp (1954) have insisted that *Triletes*, as conceived by Reinsch, has a status higher than that of a form genus and they regard it as a subdivision (*Abteilung*) of the division (*Oberabteilung*) Sporites H. Potonié. The subdivision *Triletes* includes, according to Potonié and Kremp, all megaspores and microspores without bladderlike or membranous extensions of the sexine which possess functional triradiate markings.

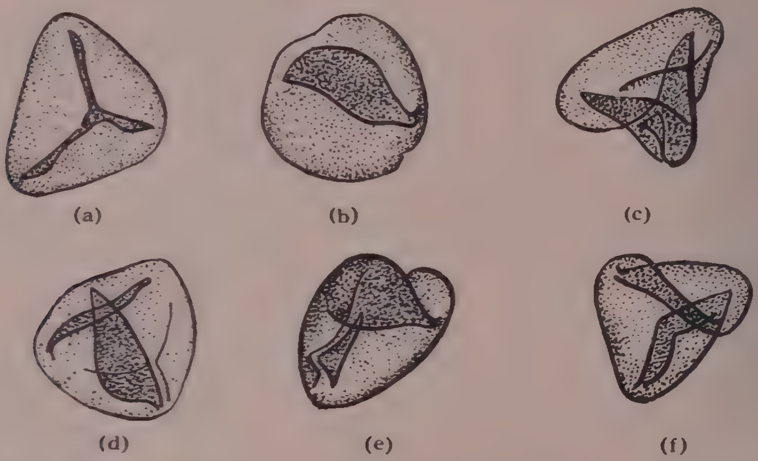

Fig. 1.—Folding patterns of the exine developed during compression of a simple thin-walled sphaerico-tetrahedral sporomorph (*Leiotriletes directus* n. spm.).

Further subdivision of trilete spores is accomplished on the basis of their size, structure, shape, and ornament; criteria which are undoubtedly largely artificial. It is true that investigations by Knox (1950) imply that the spores of the modern Lycopodiaceae and Selaginellaceae may be separated in a general way on the basis of their morphology, but that author does not suggest that her proposed classification of fossil spores, based on methods of analogy, is a natural grouping.

The existence of complex features, such as equatorial flanges, bladders, or thickenings, usually discernible even in poorly preserved or distorted specimens, probably provides the most valuable basis for a classification system. Shape and ornament, however, which are important taxonomic criteria, should be treated with caution even within the limits of an artificial system, as both are to some extent dependent on mode of preservation and maceration procedures. Compression by compacting sediments, for example, may cause spores originally sphaerico-tetrahedral to fold into shapes such as those illustrated in Figures 1(*a*)–(*f*), which can only be related to the original form after a good deal of experience in their examination. Ornament undoubtedly varies, in some plant species at least, during the development of the spores in the sporangium (Radforth 1938), but it is improbable that many immature spores occur as isolated fossils in sediments. Evidence of immaturity, however, is occasionally to be found in the spore clusters which are not infrequently observed in maceration residues. Destruction of ornamental elements during preservation or maceration is also possible, and it seems undesirable to limit too rigidly the categories of delicately ornamented forms where these categories are based on ornament alone.

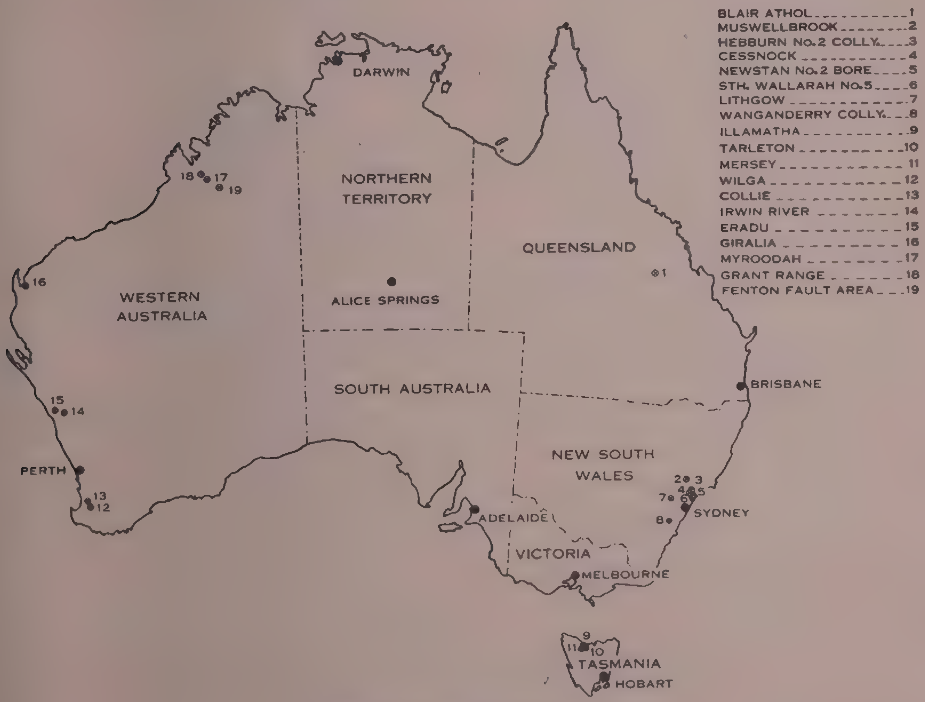

Fig. 2.—Sampling localities.

IV. Source of Samples

The New South Wales samples examined in this account were obtained by the Coal Research Section, C.S.I.R.O., during its survey of Australian coal resources, and those from other states were supplied by the Geological Survey of Western Australia and West Australian Petroleum Co. Pty. Ltd. Approximate localities of the samples examined are shown in Figure 2, although the New South Wales sampling localities were too numerous to indicate individually on the map.

V. Descriptions

Unless otherwise specified the dimensions given below are based on measurements of flattened specimens presented in full polar view. The diameter of spores with a triangular amb is taken as the mean of the lengths of the three medians.

(*a*) *Subdivision* (*Abteilung*) Triletes *Reinsch emend. Potonié & Kremp*

Leiotriletes (Naumova) Potonié & Kremp

Leiotriletes Naumova, 1937, Fig. 1.

Leiotriletes (Naum.) Potonié and Kremp, 1954, p. 120.

Leiotriletes directus n. spm.

Plate 1, Figs. 1–4; Figs. 1(*a*)–(*f*)

Probable Synonymy

P1A Dulhunty 1945.

P1A (Dulh.) de Jersey 1946.

P1A (Dulh.) Dulhunty and Dulhunty 1949.

P1A (Dulh.) Balme 1952.

Type Locality.—Seam at 688 ft, South Wallarah, No. 5 D.D.H. bore, upper part of the Newcastle Stage, N.S.W.

Dimensions (20 specimens).—Diameter 23–36 μ (mean 28 μ).

Amb triangular, sides straight or slightly convex in polar view. Trilete, scar well defined, rays straight or somewhat sinuous, extending almost to the periphery of the spore. Exine thin, subject to folding during compression, psilate or faintly granulate. Indistinct contact areas sometimes visible.

Discussion.—Widespread and often extremely abundant in Permian sediments. There is no doubt that the sporomorph *L. directus* is a very broad category embracing the spores of many plants.

Granulatisporites (Ibrahim) Potonié & Kremp

Granulatisporites Ibrahim, 1933, p. 22.

Granulatisporites (Ibr.) Potonié and Kremp, 1954, p. 126.

Granulatisporites trisinus n. spm.

Plate 1, Figs. 5–8

Probable Synonymy

P6A Dulhunty 1945.

P1B Dulhunty 1945 (in part).

P6A (Dulh.) de Jersey 1946.

P1B (Dulh.) Dulhunty and Dulhunty 1949.

P6A (Dulh.) Dulhunty and Dulhunty 1949 (in part).

P1B (Dulh.) Balme 1952.

Type Locality.—Lithgow seam, Kandos Colliery, Western Coalfield, N.S.W.

Dimensions (30 specimens).—Diameter 45–110 μ (mean 76 μ).

Amb triangular, sides slightly convex. Trilete, sutures straight or slightly sinuous extending to the periphery of the spore, lips sometimes raised or overlapping. Exine 1–2 μ thick, sexine ornamented by regular, closely packed, rounded granules about 1 μ in diameter and less than 1 μ apart. The ornament is not always distinguishable under low-power objectives and oil immersion is necessary to resolve it fully.

Discussion.—Although this sporomorph shows fairly wide variations in size the regular sexine pattern is very characteristic. *G. trisinus* occurs in samples from Western Australia, Tasmania, Queensland, and New South Wales, and is particularly common in certain seams from the Newcastle Stage.

Granulatisporites micronodosus n. spm.

Plate 1, Figs. 9–10

Probable Synonymy

P26A Dulhunty 1945 (in part).

P26A (Dulh.) de Jersey 1946.

P26A (Dulh.) Dulhunty and Dulhunty 1949.

P27A Balme 1952.

Type Locality.—Seam at 685 ft, South Wallarah No. 5 D.D.H. bore, upper part of the Newcastle Stage, N.S.W.

Dimensions (20 specimens).—Diameter 40–60 μ (mean 48 μ).

Amb triangular, sides straight or slightly convex. Trilete, sutures straight, extending to the periphery of the spore. Exine thin, distal side ornamented with rounded microverrucae about 2 μ in basal diameter, 2 μ high, and 2–3 μ apart. Ornament reduced or absent on proximal face.

Discussion.—Distinguished from *G. trisinus* by its generally smaller size and its larger and less regularly disposed ornamental processes.

Punctatisporites (Ibrahim), Potonié & Kremp

Punctatisporites Ibrahim, 1933, p. 21.

Punctatisporites (Ibr.) Potonié and Kremp, 1954, p. 120.

Punctatisporites gretensis n. spm.

Plate 2, Figs. 11–13

Probable Synonymy

P4B Dulhunty 1945 (in part).

P4B (Dulh.) Dulhunty and Dulhunty 1949 (in part).

P4F Balme 1952.

Type Locality.—Main Greta seam, Hebburn No. 2 Colliery, Greta Coal Measures, N.S.W.

Dimensions (20 specimens).—Diameter 70–154 μ (mean 118 μ).

Amb circular. Trilete, sutures straight and clearly defined extending about three quarters of the spore radius, lips prominent sometimes slightly raised, short arcuate concentric folds occasionally present at the extremities of the rays. Exine about 4 μ thick, psilate or finely granulate.

Discussion.—In New South Wales *P. gretensis* has been observed only in sediments from the Greta Coal Measures, but a similar form occurs in coals from the Collie Burn Horizon in Western Australia.

Calamospora Schopf, Wilson & Bentall

Calamospora (= *Calamitisporites* Loose 1934) Schopf, Wilson, and Bentall, 1944, p. 49.

Calamospora diversiformis n. spm.

Plate 2, Figs. 14–18

Synonymy

P4D de Jersey 1946.

P4D (de Jersey) Balme 1952.

Type Locality.—Main Greta seam, Cessnock No. 1 Colliery, Greta Coal Measures, N.S.W.

Dimensions (80 specimens).—Diameter 24–53 μ (mean 38 μ).

Amb circular, outline smooth. Trilete, sutures straight, usually extending about half the radius of the spore. Exine about 2 μ thick, psilate, or very faintly granulate. A clearly defined contact area delimited by incipient curvaturae is present in some specimens (Plate 2, Fig. 17); in others the contact area is marked by a darkened triangular thickening at the proximal pole.

Discussion.—A widely distributed Permian form which is particularly common in coals from the Greta Coal Measures in New South Wales. *C. diversiformis* is smaller than any of the sporomorphs previously assigned to *Calamospora*, but in other respects it conforms with the original generic diagnosis. There is, of course, no suggestion that *C. diversiformis* derives from Calamarian fructifications and, in fact, it bears a marked resemblance to the Mesozoic and Tertiary spores assigned by Cookson (1953) to *Sphagnites*. Spores of similar appearance have been illustrated also by Luber (1939), from coals of the Kuznetsk and Minussinsk basins.

Apiculatisporites (Ibrahim *non* Bennie & Kidston) Potonié & Kremp

Apiculatisporites Ibrahim, 1933, p. 23.

Apiculatisporites (Ibr.) Potonié and Kremp, 1954, p. 130.

Apiculatisporites levis n. spm.

Plate 2, Figs. 19–21

Synonymy

P29C Balme 1952.

Type Locality.—Main seam, Proprietary Colliery, Collie Horizon, Collie, W.A.

Dimensions (18 specimens).—Diameter 22–37 μ (mean 25 μ).

Amb circular. Trilete, sutures straight, extending to the periphery of the spore. Exine thin, ornamented with small spines or pustules about 1 μ in height, 1–2 μ in basal diameter, irregularly distributed over the surface of the spore. Proximal contact area usually discernible, ornament reduced on proximal face.

Discussion.—Identified only from a few localities from the lowest coal horizon at Collie, but often common in the samples in which it does occur.

Apiculatisporites filiformis n. spm.

Plate 2, Figs. 22–23

Type Locality.—Seam at 688 ft, South Wallarah No. 5 D.D.H. bore, upper part of the Newcastle Stage, N.S.W.

Dimensions (20 specimens).—Diameter 26–46 μ (mean 42 μ).

Amb circular or subcircular. Trilete, sutures indistinct, extending to periphery of spore. Sexine ornamented with aciculate or filiform processes 1–2 μ in basal diameter and up to 5 μ in length. Spine density variable, but individual spines usually about 5 μ apart.

Discussion.—To date identified only in coals from the Newcastle Stage in New South Wales. *A. filiformis* differs from *Acanthotriletes tereteangulatus* n. spm. in its broadly circular outline and longer ornamental processes.

Apiculatisporites cornutus n. spm.

Plate, 2, Figs. 24–26

Type Locality.—Main Greta seam, Cessnock No. 1 Colliery, Greta Coal Measures, N.S.W.

Dimensions (20 specimens).—Diameter 31–45 μ (mean 36 μ).

Amb circular or subcircular. Trilete, sutures indistinct, slightly sinuous, extending almost to the periphery of the spore. Exine fairly thick, ornamented with heavy, irregularly disposed, conical or mammilate processes, occasionally bifurcate at the tips. Processes 1–4 μ in basal diameter, 3–5 μ high.

Discussion.—Fairly common in seams of the Greta Coal Measures of New South Wales but, apart from a few comparable specimens in the Irwin River coals, has not been observed elsewhere.

Acanthotriletes (Naumova) Potonié & Kremp

Acanthotriletes Naumova, 1937, Fig. 1.

Acanthotriletes (Naum.) Potonié and Kremp, 1954, p. 133.

Acanthotriletes tereteangulatus n. spm.

Plate 2, Figs. 27–29

Synonymy

P17B Balme 1952.

Type Locality.—Moira seam, Black Diamond Lease, Collie Horizon, Collie, W.A.

Dimensions (40 specimens).—Diameter 24–41 μ (mean 32 μ).

Amb rounded triangular, sides usually slightly concave. Trilete, sutures straight, extending almost to the periphery of the spore. Exine frequently distorted by compression, ornamented by short spines varying between 1 μ and 4 μ in length, irregularly disposed over the surface of the spore.

Discussion.—*A. tereteangulatus* is widely distributed in Permian sediments. It is important in the Collie beds, where its occurrence in large numbers characterizes the coals of the Collie Horizon. Similar forms have been illustrated by Ghosh and Sen (1948, Plate 4, Figs. 28, 29, 31) from the Raniganj coals in India.

Acanthotriletes ericianus n. spm.

Plate 3, Figs. 30–33

Probable Synonymy

P16A Dulhunty 1945.

P16A (Dulh.) de Jersey 1946.

P16A (Dulh.) Dulhunty and Dulhunty 1949.

Type Locality.—Lithgow seam, Wallerawang Colliery, Western Coalfield, N.S.W.

Dimensions (40 specimens).—Diameter 39–84 μ (mean 59 μ). Polar axis 36–60 μ.

Amb triangular, sides straight or slightly convex. Cordate in lateral compression, proximal face triangular and distal side rounded. Trilete, rays extending to periphery of spore, lips often out-turned or overfolded. Exine 1–2 μ thick, ornamented on the distal side with acicular or acuminate processes about 2 μ in basal diameter and up to 7 μ long. Disposition of the spines varies considerably between specimens. Proximal surface psilate or with greatly reduced ornament.

Discussion.—*A. ericianus* is a very common form in most coals from the Newcastle and Tomago Stages in New South Wales but has rarely been observed in separations from other sampling localities. From Luber's (1939, Tables I and II, C4) illustration the sporomorph *Turriella rigidispina* Luber from the Kuznetsk and Minussinsk basins appears to be very similar to *A. ericianus*.

Acanthotriletes dentatus n. spm.

Plate 3, Fig. 34

Type Locality.—Seam at 755 ft. Newstan No. 2 D.D.H. bore, upper part of the Newcastle Stage, N.S.W.

Dimensions (20 specimens).—Diameter 78–114 μ (mean 98 μ).

Amb rounded triangular, sporomorph often fragmentary. Trilete, sutures straight, extending to periphery of spore. Exine about 2 μ thick ornamented with heavy, closely packed conical processes 3–4 μ in basal diameter and 5–7 μ long. Pyramidal proximal surface unornamented.

Discussion.—An uncommon but distinctive form from the Newcastle Stage of New South Wales. *A. dentatus* is larger and more heavily ornamented than *A. ericianus*.

Acanthotriletes villosus n. spm.

Plate 3, Figs. 37–38

Synonymy

P17C Balme 1952.

Type Locality.—Lithgow seam, Kandos Colliery, Western Coalfield, N.S.W.

Dimensions (28 specimens).—Diameter 68–98 μ (mean 85 μ).

Amb rounded triangular, often distorted by compression. Trilete, sutures extending to periphery of the spore, margins of the sutures frequently overfolded. Exine about 2 μ thick, ornamented with closely packed spines or baculae about 1 μ in basal diameter and 2–3 μ high.

Discussion.—A rare but striking sporomorph from the Newcastle Stage of New South Wales and the Collie Burn Horizon in Western Australia.

Acanthotriletes uncinatus n. spm.

Plate 3, Figs. 35–36

Type Locality.—Seam at 688 ft, South Wallarah No. 5 D.D.H. bore, upper part of the Newcastle Stage, N.S.W.

Dimensions (12 specimens).—Diameter 28–46 μ (mean 38 μ).

Amb triangular, sides straight and apice sharply rounded. Trilete, sutures extending almost to the periphery of the spore, lips sometimes slightly out-turned. Exine about 2 μ thick, sexine echinate, individual spines 1–2 μ in basal diameter, 2–8 μ long, usually uncinate.

Discussion.—A rare form observed only in Newcastle Stage sediments. Distinguished from *A. ericianus* by its smaller size and sharply angular outline, and from *A. tereteangulatus* by its thicker exine and longer, more densely packed spines.

Acanthotriletes ramosus n. spm.

Plate 3, Figs. 39–41

Synonymy

P27B Balme 1952.

Type Locality.—Main seam, Proprietary Colliery, Collie Horizon, Collie, W.A.

Dimensions (12 specimens).—Diameter 26–45 μ (mean 35 μ).

Amb triangular, sides slightly convex, often distorted and preserved in lateral compressions. Trilete, sutures extending almost to the periphery of the spore. Exine thin, ornamented with coarse spines or baculae often bifurcate at the tips and occasionally joined together at their bases. Ornamental processes 2–5 μ in basal diameter, 2–7 μ long.

Discussion.—Observed first in coals from the Collie Horizon in Western Australia, but subsequently found in samples from the Newcastle Stage and the Collie Burn Horizon. The ornament of *A. ramosus* is similar to that of sporomorphs placed in the form genus *Raistrickia* by Schopf, Wilson, and Bentall (1944). The diagnosis of *Raistrickia*, however, specifies a circular outline and thick exine.

Verrucosisporites (Ibrahim) Potonié & Kremp

Verrucosisporites Ibrahim, 1933, p. 25.

Verrucosisporites (Ibr.) Potonié and Kremp, 1954, p. 137.

Verrucosisporites pseudoreticulatus n. spm.

Plate 4, Figs. 42–44

Type Locality.—Muswellbrook seam, Muswellbrook Open Cut, Greta Coal Measures, N.S.W.

Dimensions (20 specimens).—Diameter 63–115 μ (mean 81 μ).

Amb subcircular or rounded triangular. Trilete, sutures straight extending almost to the periphery of the spore, lips sometimes slightly raised. Exine 2–3 μ thick ornamented with closely packed low dome-shaped protruberances 2–3 μ in basal diameter and 1–3 μ high.

Discussion.—A common sporomorph in the Greta Coal Measures of New South Wales. Comparable but possibly slightly differing forms occur in coals from Tarleton, Tas., and Collie, W.A. Under low-power objectives it is not always easy to distinguish from some specimens of *Tholosporites parvitholus* n. spm. (q.v.).

Verrucosisporites bullatus n. spm.

Plate 4, Figs. 45–47

Type Locality.—Seam at 688 ft, South Wallarah No. 5 D.D.H. bore, upper part of the Newcastle Stage, N.S.W.

Dimensions (20 specimens).—Diameter 36–50 μ (mean 43 μ).

Amb rounded triangular or subcircular. Trilete, sutures straight, indistinct, extending to the periphery of the spore. Exine ornamented with bulbous processes slightly contracted at their bases; ornamental elements larger in a narrow equatorial zone. Proximal surface pyramidal, psilate, or with reduced ornament.

Discussion.—A fairly common sporomorph in the Newcastle Stage of New South Wales but not identified elsewhere.

Verrucosisporites trisecatus n. spm.

Plate 4, Figs. 48–49; Plate 5, Fig. 50

Probable Synonymy

P29B Dulhunty 1945 (in part).

Type Locality.—Seam at 719 ft, South Wallarah No. 2 borehole, Newcastle Stage, N.S.W.

Dimensions (30 specimens).—Diameter 65–135 μ (mean 103 μ).

Amb circular, outline irregular. Trilete, sutures of variable length, in many specimens extending on to the distal surface and tending to trisect the spore. Exine dense, about 2 μ thick, and ornamented with closely packed generally hemispherical verrucae of rather variable size. Individual processes 3–7 μ in basal diameter, 1–4 μ high.

Discussion.—A fairly common form in Newcastle Stage sediments and occasionally specimens have been found in Tomago Stage coals. A very similar and probably identical form occurs in coal from the Liveringa Formation in the Kimberley District of Western Australia.

Verrucosisporites parmatus n. spm.

Plate 5, Figs. 51–52

Probable Synonymy

P29A Dulhunty 1945 (in part).

P29A (Dulh.) de Jersey 1946 (in part).

P29A (Dulh.) Dulhunty and Dulhunty 1949 (in part).

Type Locality.—Main Greta seam, Cessnock No. 1 Colliery, Greta Coal Measures, N.S.W.

Dimensions (20 specimens).—Diameter 32–52 μ (mean 42 μ).

Amb circular, outline irregular. Trilete, sutures straight, extending to periphery of spore, proximal contact area clearly defined. Exine thin, ornamented on distal side by rounded verrucae or pustules 2–5 μ in basal diameter, about 2 μ high, and 3–4 μ apart. In some specimens a slight increase in the size of the ornamental processes occurs in the region of the distal pole. Contact area unornamented.

Discussion.—Observed only in sediments from the Greta Coal Measures in New South Wales. *V. parmatus* differs from *Apiculatisporites levis* in its larger size and more prominent ornament.

Microreticulatisporites (Knox) Potonié & Kremp

Microreticulatisporites Knox 1950, p. 319.

Microreticulatisporites (Knox) Potonié and Kremp 1954, p. 143.

Microreticulatisporites bitriangularis n. spm.

Plate 5, Figs. 53–54

Type Locality.—Borehole seam, Burwood Colliery, Newcastle Stage, N.S.W.

Dimensions (20 specimens).—Diameter 25–35 μ (mean 31 μ).

Amb triangular, sides slightly convex. Trilete, sutures straight or slightly sinuous, extending almost to the periphery of the spore. Proximal face bearing three narrow crescentic folds or thickenings extending from the apices, and concave towards the proximal pole. Exine thin, microreticulate, muri about 1 μ wide, lumens 1–2 μ in diameter on the proximal face and usually a little larger on the distal.

Discussion.—Fairly common in certain coals from the Newcastle Stage and seen also in macerations from a carbonaceous shale from Eradu, W.A. *M. bitriangularis* resembles in structure the sporomorph *Ahrenisporites guerickei* (Horst) Potonié & Kremp but, because of its well-defined sculpture and the fact that the proximal crescentic thickenings are not clearly developed in all specimens,, it has been placed in *Microreticulatisporites*.

Camptotriletes (Naumova) Potonié & Kremp

Camptotriletes Naumova, 1937, Fig. 1.

Camptotriletes (Naum.) Potonié and Kremp, 1954, p. 142.

Camptotriletes biornatus n. spm.

Plate 5, Figs. 55–56

Type Locality.—Homeville seam, Lower Split, Hebburn No. 1 Colliery, Greta Coal Measures, N.S.W.

Dimensions (20 specimens).—Diameter 89–127 μ (mean 104 μ).

Amb circular or rounded triangular. Trilete, sutures extending to the periphery of the spore, lips usually slightly raised. Exine about 4 μ thick, distal side ornamented with coarse verrucae 4–8 μ in diameter and about 4 μ high, verrucae often joined by shallow muri to form rudimentary cristae. Proximal side granulate, verrucate, or with irregular ridges.

Discussion.—A distinctive form observed only in Greta Coal Measures sediments.

(*b*) *Subdivision* (*Abteilung*) Zonales *Bennie & Kidston emend. Potonié & Kremp*

Cirratriradites (Wilson & Coe) Potonié & Kremp

Cirratriradites Wilson and Coe, 1940, p. 183.

Cirratriradites (Wilson & Coe) Potonié and Kremp, 1954, p. 162.

Cirratriradites splendens n. spm.

Plate 5, Figs. 57–59; Plate 6, Figs. 60–61

Probable Synonymy

P32A Dulhunty 1945.

P32A (Dulh.) Dulhunty and Dulhunty 1949.

P32B Balme 1952.

Type Locality.—Main Greta seam, Hebburn No. 2 Colliery, Greta Coal Measures, N.S.W.

Dimensions (70 specimens).—Total diameter 59–142 μ (mean 87 μ), central body 41–67 μ (mean 53 μ).

Spore complex, consisting of a central body surrounded by an equatorially attached membraneous wing. Central body circular or subtriangular in polar view, equatorial flange translucent, sometimes with radially arranged thickenings which merge into a band of thickened exine marking the junction of body and wing. Trilete, sutures extending to the line of junction of the wing. Exine of central body granulate and ornamented on the distal side by flattened verrucae or conical processes of very variable size and form. In some specimens similar processes are also present on the wing (Plate 6, Fig. 60).

Discussion.—*C. splendens* is a very variable form which occurs in many of the samples examined. The largest and best-preserved specimens were obtained from the Greta Coal Measures of New South Wales, those from the Newcastle and Tomago Stages and the West Australian localities having narrower wings and less pronounced ornament. It may eventually be desirable to separate the sporomorph into two forms for stratigraphical purposes.

(c) *Subdivision* (*Abteilung*) Saccites *Erdtmann*

Nuskoisporites Potonié & Klaus

Nuskoisporites Potonié and Klaus, 1954, p. 528.

The two sporomorphs described below are assigned to *Nuskoisporites* although there is some doubt as to whether they strictly conform to the generic diagnosis. The equatorial limbus, which Potonié and Klaus regard as particularly significant, is seldom clearly exhibited, although it is discernible in some well-preserved specimens (Plate 8, Fig. 68). The Australian sporomorphs also have a much thinner exine than *Nuskoisporites dulhuntyi* Potonié & Klaus and often do not show the trilete scar clearly. Nevertheless Potonié and Klaus obviously regard Dulhunty's types 34A, 34B, and 34C as belonging to *Nuskoisporites* and the generally poor preservation of the Australian material must also be considered when assessing the taxonomic significance of morphological variations.

Nuskoisporites gondwanensis n. spm.

Plate 6, Figs. 62–65; Plate 7, Figs. 66–67

Probable Synonymy

P34A Dulhunty 1945.

P34B Dulhunty 1945.

P34B (Dulh.) Dulhunty and Dulhunty 1949.

P34A (Dulh.) Balme 1952 (in part).

Type Locality.—Big Ben seam, Bloomfield Colliery, Tomago Stage, N.S.W.

Dimensions (75 specimens).—Total diameter 74–210 μ (mean 129 μ), central body 60–122 μ (mean 88 μ).

Spore complex, consisting of a central body surrounded by an equatorially disposed inflated bladder, proximal and distal sides free. Central body circular in polar view. Trilete, sutures usually indistinct, extending about half the length of the radius, sometimes open forming a triangular rent in the proximal face. Exine of central body thin, subject to rupture and folding, granulate or finely punctate. Equatorial bladder of variable width, overlapping the body in compressed specimens giving the appearance of two or more concentric margins around the periphery of the central body. Bladder possesses a strong infra-reticulum in which radial elements are often strongly developed to give a characteristic pattern.

Discussion.—Although it is seldom abundant in any one sample *N. gondwanensis* is without doubt one of the most important sporomorphs from the Australian Permian. It occurs in sediments from all Australian States from which samples were available, and many of the Indian types figured and described by Virkki (1945, cf. types 43–55) would also fall into the sporomorph as defined above. Cookson (personal communication) has observed *N. gondwanensis* as a remanié fossil in Tertiary sediments from Victoria, but as far as is known, it does not occur *in situ* in deposits of younger age than Permian.

Nuskoisporites rotatus n. spm.

Plate 8, Figs. 68–71

Probable Synonymy

P34C Dulhunty 1945.

P34B (Dulh.) Balme 1952 (in part).

Type Locality.—Main Greta seam, Hebburn No. 2 Colliery, Greta Coal Measures, N.S.W.

Dimensions (25 specimens).—Total diameter 80–168 μ (mean 125 μ), central body 58–122 μ (mean 94 μ).

Spore body complex, consisting of a central body surrounded by an equatorially attached inflated bladder. Central body circular, subcircular or nearly oval in polar view. Trilete, sutures usually clear and of variable length sometimes extending to the periphery of the central body, frequently open at the proximal pole. Exine of central body thin, finely punctate, usually torn and folded. Equatorial bladder thin, 10–20 μ wide overlapping the central body by about 5–10 μ in compressed specimens, ornamented by an extremely fine infra-reticulum giving it a punctate appearance. A "limbus" or thickening about 5 μ wide is sometimes present around the outer margin of the bladder (Plate 8, Fig. 68).

Discussion.—Most common in coals from the Greta Coal Measures but occasionally observed elsewhere, particularly in some samples from the Collie Burn horizon. *N. rotatus* differs from *N. gondwanensis* in its narrower and more finely ornamented bladder.

Tholosporites n. spt.

The name *Tholosporites* is proposed for sporomorphs of unknown affinities having the following characteristics:

Amb triangular, subtriangular or circular. Trilete with clearly defined sutures. Exine fairly thick, micro-reticulate, striato-reticulate, or striato-granulate. Sexine extended to form three hemispherical or flattened blisters situated near the proximo-distal margin at about the middle of the inter-radial areas in specimens flattened in polar view. The three blisters are foci for the ornamental elements which radiate from each of them to form a ternate pattern.

Derivation of name.—Gk. θόλος, a cupola or dome.

Tholosporites egregius n. spm. is designated as the genotype.

Tholosporites egregius n. spm.

Plate 9, Figs. 72–75

Synonymy

P21A Dulhunty 1945.

P21A (Dulh.) Balme 1952.

Type Locality.—Seam at 755 ft. Newstan No. 2 D.D.H. bore, Newcastle Stage, N.S.W.

Dimensions (70 specimens).—Diameter 70–130 μ (mean 106 μ).

Amb rounded triangular. Trilete, sutures clearly defined extending to the periphery of the spore and sometimes passing on to the distal face. Exine about 3 μ thick. Sexine extended into three hemispherical blisters up to 40 μ in basal diameter and 7–20 μ high. These blisters are situated at the proximo-distal margins at the middle of the inter-radial areas. Exine ornament complex, consisting of striate ridges about 1 μ wide which arise on the blisters and radiate from them, anastomising in the polar areas to form an irregular reticulum.

Discussion.—T. egregius is a sporomorph of striking appearance which appears to have stratigraphical importance. In New South Wales it has been found only in the Newcastle and Tomago Stages, but it occurs also in the upper coals at Collie and, in large numbers, in coal from the Liveringa Formation in the Kimberley district of Western Australia. It seems to occur only in clean bright coals so that its distribution may be controlled by environmental or edaphic factors which cannot yet be fully assessed. Slight differences in size and ornament were noted between the New South Wales and Western Australian specimens, but these may perhaps be attributed to variations in the conditions of preservation.

In his original illustration of type 21A, Dulhunty (1945, p. 151) showed a conical appendage arising in the centre of each blister, but no such processes were observed on any of the specimens examined by the authors.

Tholosporites parvitholus n. spm.

Plate 10, Figs. 76–80

Type Locality.—Lithgow seam, State Colliery, Lithgow, Western Coalfield, N.S.W.

Dimensions (50 specimens).—Diameter 47–95 μ (mean 72 μ).

Amb circular or rounded triangular. Trilete, sutures straight, clearly defined, extending to the periphery of the spore and in some specimens on to the distal face. Exine about 2 μ in thickness, sexine extended into three inter-radial blisters up to 15 μ in diameter and about 3 μ high. The development of these blisters is not a constant feature and they are not discernible on some specimens agreeing in other particulars with this diagnosis. Sexine ornament microreticulate with muri about 1 μ wide enclosing lumens 1–3 μ in diameter. In the vicinity of the blisters the lumens show some tendency to parallel arrangement, radiating outwards.

Discussion.—T. parvitholus is an extremely common spore in certain coals from the Newcastle and Tomago Stages in New South Wales and occurs also in the Liveringa Formation in Western Australia. It is almost invariably associated with *T. egregius* in New South Wales sediments but the fact that it does not occur in the Collie coals implies that the two sporomorphs were produced by different plants and not, as was at first suspected, that *T. parvitholus* represents an immature or abortive form of *T. egregius*.

Bascanisporites n. spt.

The name *Bascanisporites* is proposed for sporomorphs of unknown affinity having the following characteristics:

Spore body complex, consisting of a circular or oval central body surrounded by an equatorially attached bladder. Germinal mechanism obscure; although some specimens bear a short-rayed trilete scar which is possibly non-functional. Exine of central body dense, about 2 μ thick, psilate or finely granulate. Bladder attached along a narrow equatorial zone, external margin usually lobate, but circular in some specimens. Bladder finely infra-reticulate.

Derivation of name.—Gk. βασκαν, an amulet or charm.

Bascanisporites undosus n. spm. is designated as the genotype.

Bascanisporites undosus n. spm.

Plate 10, Figs. 81–83

Type Locality.—Seam at 688 ft, South Wallarah No. 2 D.D.H. bore, Newcastle Stage, N.S.W.

Dimensions (30 specimens).—Total diameter 60–89 μ (mean 77 μ), central body 48–66 μ (mean 58 μ).

Spore body complex, consisting of a central body surrounded by an equatorially attached bladder, proximal and distal sides free. Many specimens show no tetrad markings, in others a faint trilete scar is visible. Exine of central body dark in colour, about 2 μ thick, sometimes ruptured; psilate or faintly marked. Bladder overlapping central body by about 5 μ in proximo-distal compressions, external periphery of bladder usually lobate with up to five clearly developed lobes; occasional specimens, however, possess a single circular bladder. In others the bladder is non-continuous and individual specimens have a polysaccate appearance. Bladder ornamented with a fine infra-reticulum.

Discussion.—As far as is known *B. undosus* is confined to coals from the upper part of the Newcastle Stage in New South Wales. Its distribution is sporadic and although it was very abundant in some of the samples examined it was only occasionally encountered in the majority.

VI. Distribution of Sporomorphs

Table 1 shows the distribution of the sporomorphs described in Section V, although it must be emphasized that many of the source samples are not directly comparable, varying as they do between clean bright coal and predominantly inorganic clastic sediments. At this stage it is impossible to attempt any assessment of the relationships between facies changes and microfloral variations although such relationships undoubtedly exist. In the Newcastle Stage of New South Wales, for example, the spore assemblages of the shales are composed predominantly of bisaccate pollen grains of the *Lueckisporites* type, while trilete and monocolpate sporomorphs make up a high proportion of the individual assemblages in the coals. It may be inferred from this that many of the trilete forms represent the remnants of an autochthonus "coal swamp" flora, and that the bisaccate grains are chiefly wind-blown forms which have been, in part at least, derived from elements of an "upland" flora.

In New South Wales the sediments of the Greta Coal Measures may be readily distinguished from those of the Upper Coal Measures on a palynological basis,

TABLE 1

DISTRIBUTION OF TRILETE SPOROMORPHS IN AUSTRALIAN PERMIAN SEDIMENTS

Sporomorph	N.S.W.			Qld.	Tas.		Western Australia									
							South West						N.W. Basin	Desert Basin		
	Newcastle Stage	Tomago Stage	Greta Stage	Blair Athol (U. Bowen)	Mersey Coals	Mt. Pelion	Collie (Cardiff horizon)	Collie (Collie Burn horizon)	Collie (Collie horizon)	Wilga	Irwin River	Eradu	Giralia (?Bulgadoo Fm.)	Myroodah	Grant Range (Grant Fm.)	Fenton Fault-area (Liveringa Fm.)
Leiotriletes directus	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+
Granulatisporites trisinus	+	+	+	+		+	+	+				+	+	+	+	+
G. micronodosus	+	+	+	+			+	+	+							+
Punctatisporites gretensis			+					+								
Calamospora diversiformis	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+
Apiculatisporites levis								+	+		+					
A. filiformis	+															
A. cornutus			+								?					
Acanthotriletes tereteangulatus	+			+		+	+	+	+	+	+	+	+	+	+	
A. ericianus	+	+	+	+				+								
A. dentatus	+															
A. villosus	+						+	+								
A. uncinatus	+	+														
A. ramosus	+								+			+		+	+	
Verrucosisporites pseudoreticulatus			+		+											
V. bullatus	+															
V. trisecatus	+															+
V. parmatus			+													
Microreticulatisporites bitriangularis	+											+				
Camptotriletes biornatus			+													
Cirratriradites splendens	+		+					+	+				+	+	?	
Nuskoisporites gondwanensis	+	+	+		+		+	+					+		+	+
N. rotatus	+	+	+		+		+	+								
Tholosporites egregius	+	+						+								+
T. parvitholus	+	+														+
Bascanisporites undosus	+															

and there are some indications that further work will enable the Upper Coal Measures themselves to be zoned in a broad way. Any attempt at Australia-wide correlations, however, would be premature, although the spore and pollen distributions recorded so far do indicate an essential palaeofloristic unity over the whole of the Australian continent in Upper Permian times. There is, for example, a notable resemblance between the spore floras of the Newcastle Stage and those of the upper coals at Collie and the Liveringa Formation in the Desert Basin of Western Australia.

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Explanation of Plates 1–10

Unless otherwise specified magnifications are × 500

Plate 1

Figs. 1–2.—*Leiotriletes directus.* Proximal view.
Fig. 3.—*L. directus.* Folded specimen.
Fig. 4.—*L. directus.* Two specimens, one compressed proximo-distally and the other laterally.
Figs. 5–7.—*Granulatisporites trisinus.*
Fig. 8.—*G. trisinus.* Tetrad.
Fig. 9.—*Granulatisporites micronodosus.* Proximal view.
Fig. 10.—*G. micronodosus.* Lateral view.

Plate 2

Figs. 11–13.—*Punctatisporites gretensis.* Proximal view.
Figs. 14–16.—*Calamospora diversiformis.* Proximal view.
Fig. 17.—*C. diversiformis.* Semilateral view.
Fig. 18.—*C. diversiformis.* Lateral view.
Fig. 19.—*Apiculatisporites levis.*
Fig. 20.—*A. levis.* Showing contact area.
Fig. 21.—*A. levis.*
Figs. 22–23.—*Apiculatisporites filiformis.*
Figs. 24–26.—*Apiculatisporites cornutus.*
Figs. 27–29.—*Acanthotriletes tereteangulatus.*

Plate 3

Fig. 30.—*Acanthotriletes ericianus.*
Fig. 31.—*A. ericianus.* Torn specimen.
Fig. 32.—*A. ericianus.*
Fig. 33.—*A. ericianus.* Lateral view showing psilate proximal area.
Fig. 34.—*Acanthotriletes dentatus.* Lateral view.
Figs. 35–36.—*Acanthotriletes uncinatus.*
Figs. 37–38.—*Acanthotriletes villosus.*
Fig. 39.—*Acanthotriletes ramosus.* Proximal view.
Figs. 40–41.—*A. ramosus.* Lateral view.

Plate 4

Figs. 42–43.—*Verrucosisporites pseudoreticulatus.*
Fig. 44.—*V. pseudoreticulatus.* Lateral view.
Figs. 45–47.—*Verrucosisporites bullatus.* Polar view.
Figs. 48–49.—*Verrucosisporites trisecatus.* Proximal view.

PLATE 5

Fig. 50.—*Verrucosisporites trisecatus.* Proximal view.
Fig. 51.—*Verrucosisporites parmatus.* Proximal view showing contact area.
Fig. 52.—*V. parmatus.* Polar view.
Figs. 53–54.—*Microreticulatisporites bitriangularis.* Polar view.
Fig. 55.—*Camptotriletes biornatus.* Polar view showing distal ornament.
Fig. 56.—*C. biornatus.*—Proximal face.
Figs. 57–59.—*Cirratriradites splendens.*

PLATE 6

Figs. 60–61.—*Cirratriradites splendens.* Large forms.
Figs. 62–63.—*Nuskoisporites gondwanensis.* Polar view.
Fig. 64.—*N. gondwanensis.* Semi-lateral view.
Fig. 65.—*N. gondwanensis.* Proximal view.

PLATE 7

Figs. 66–67.—*Nuskoisporites gondwanensis.* Large forms.

PLATE 8

Fig. 68.—*Nuskoisporites rotatus.* Proximal view showing marginal limbus.
Figs. 69–71.—*N. rotatus.*

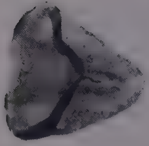
PLATE 9

Figs. 72–74.—*Tholosporites egregius.* Proximal view.
Fig. 75.—*T. egregius.* Lateral view.

PLATE 10

Figs. 76–79.—*Tholosporites parvitholus.* Proximal view.
Fig. 80.—*T. parvitholus.* Sexine ornament.
Figs. 81–83.—*Bascanisporites undosus.* Polar view.

PERMIAN TRILETE SPOROMORPHS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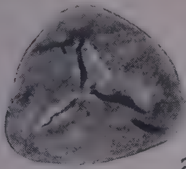
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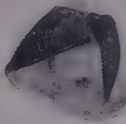
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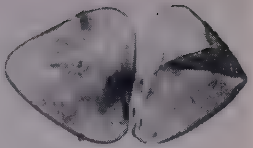
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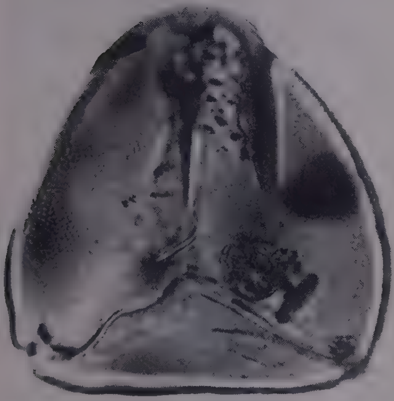
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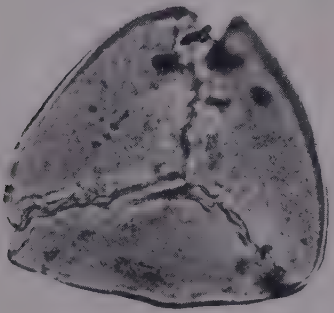
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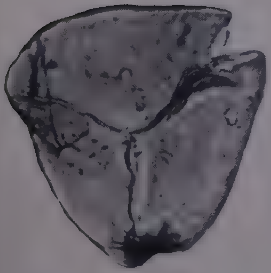
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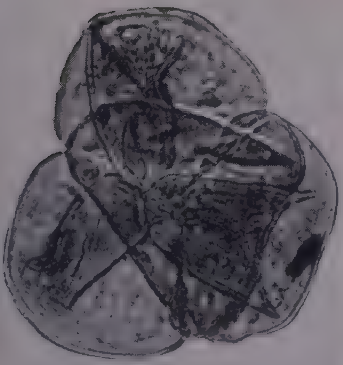
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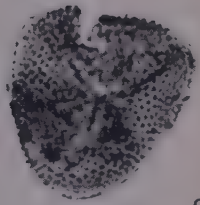
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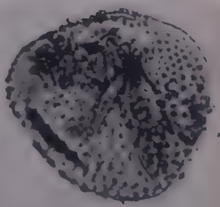
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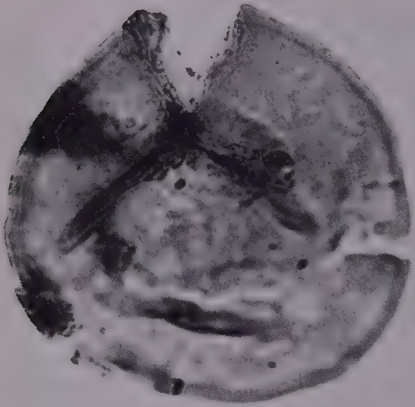
PERMIAN TRILETE SPOROMORPHS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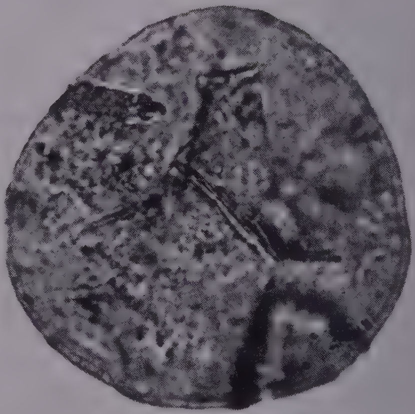
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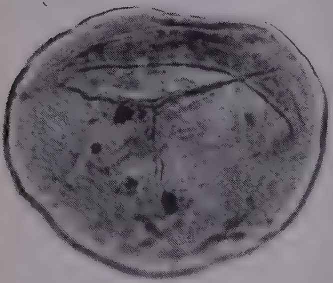
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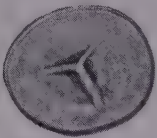
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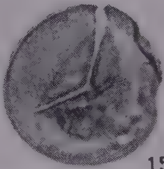
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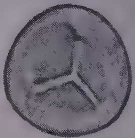
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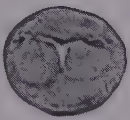
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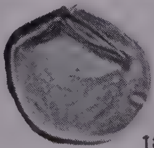
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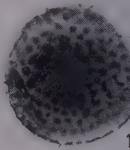
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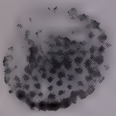
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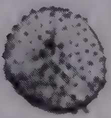
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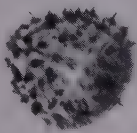
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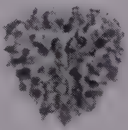
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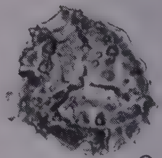
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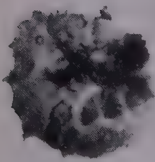
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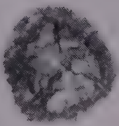
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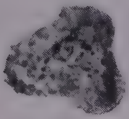
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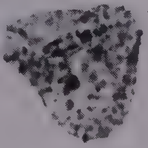
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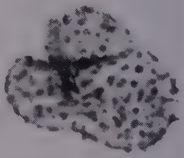
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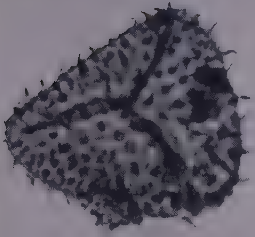
PERMIAN TRILETE SPOROMORPHS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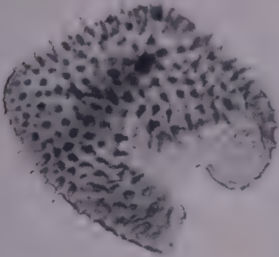
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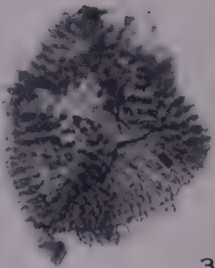
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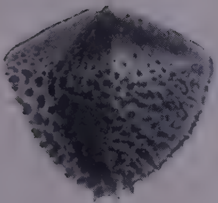
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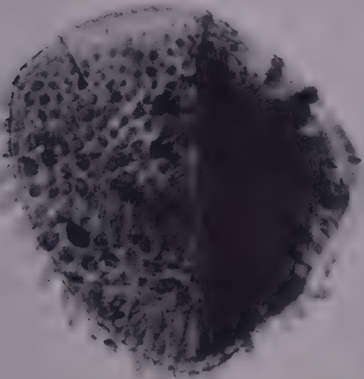
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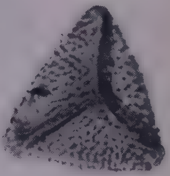
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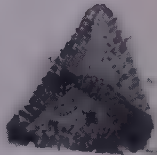
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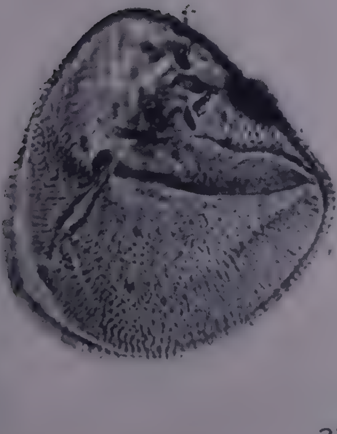
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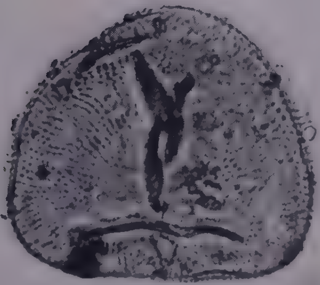
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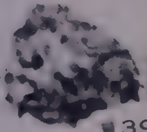
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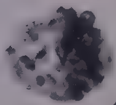
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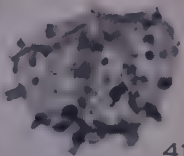
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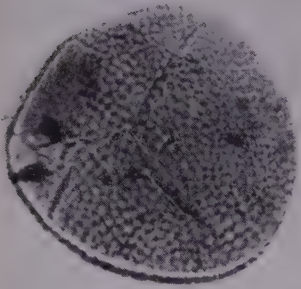

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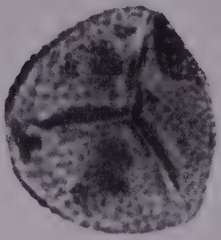

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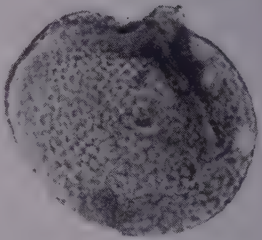

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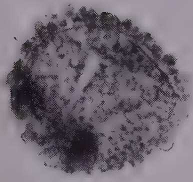

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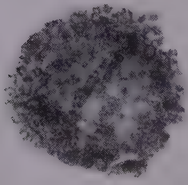

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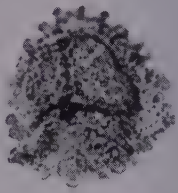

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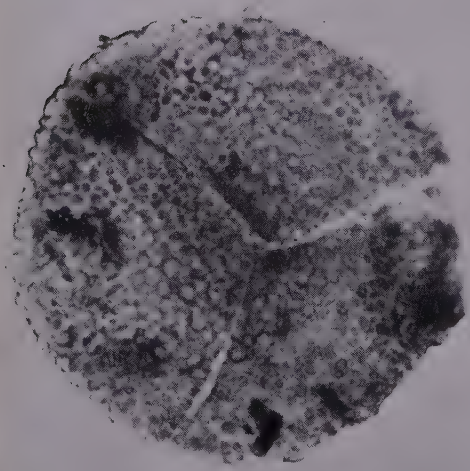

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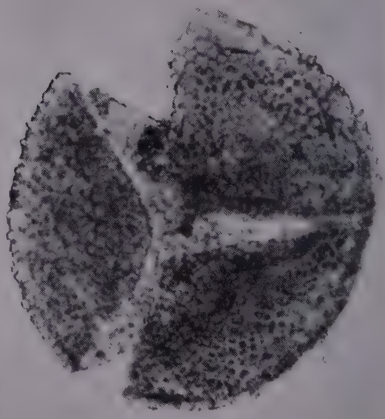

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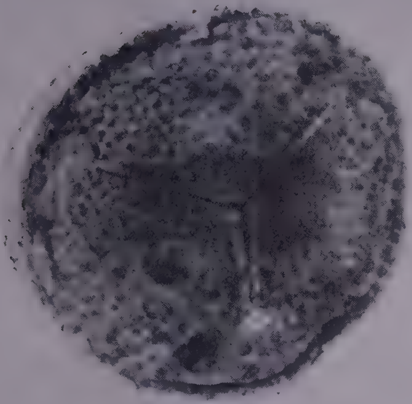
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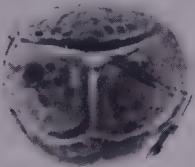
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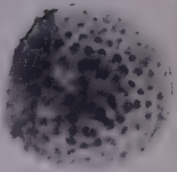
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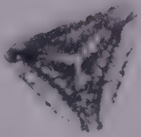
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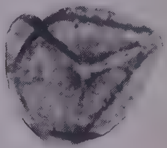
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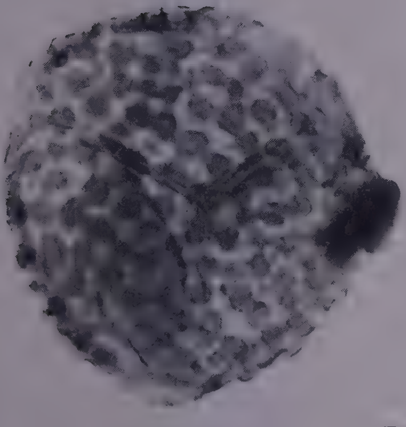
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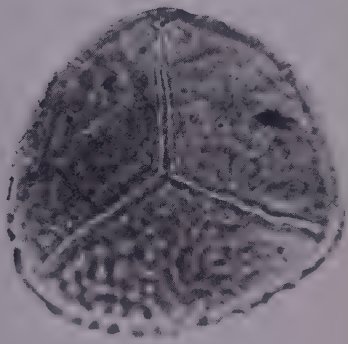
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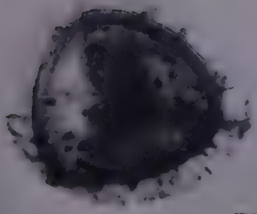
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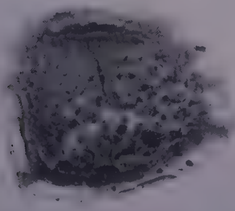
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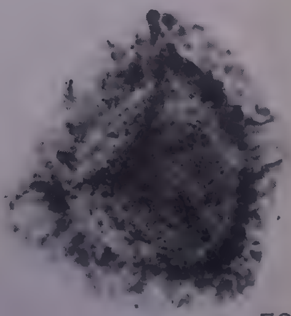
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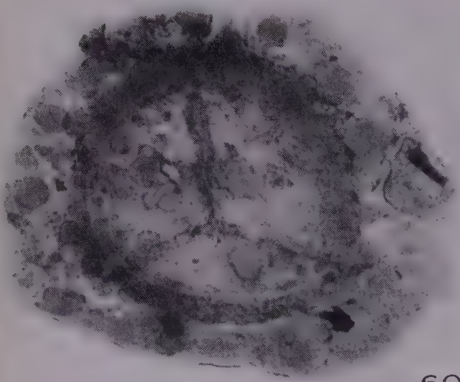

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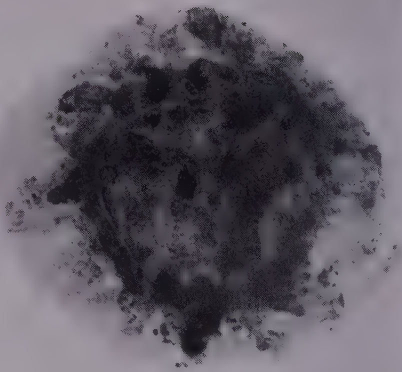

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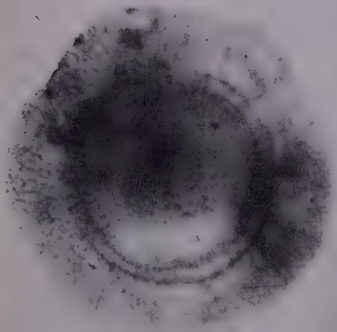

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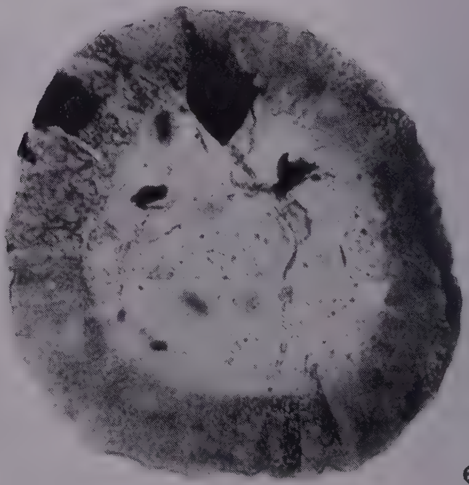

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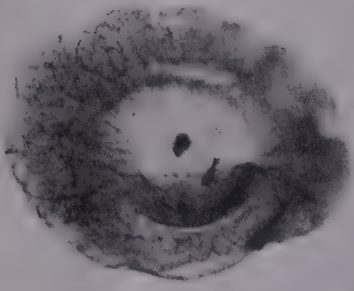

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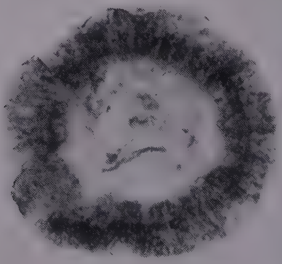

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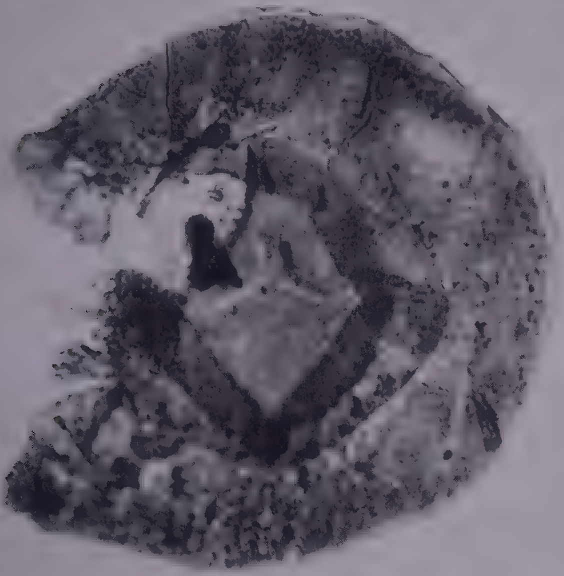

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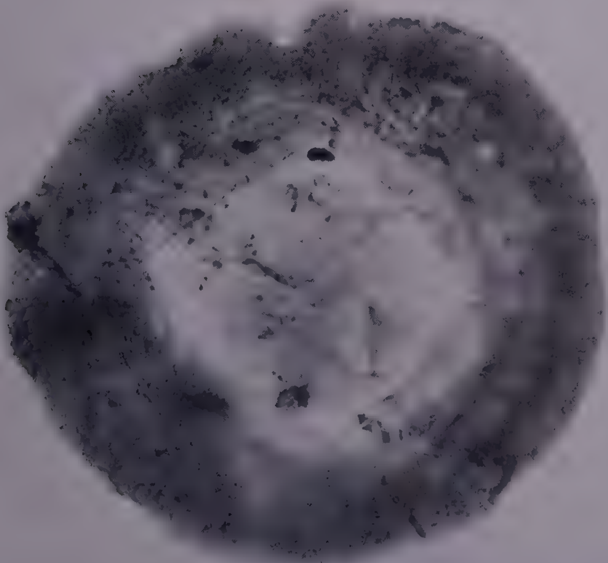

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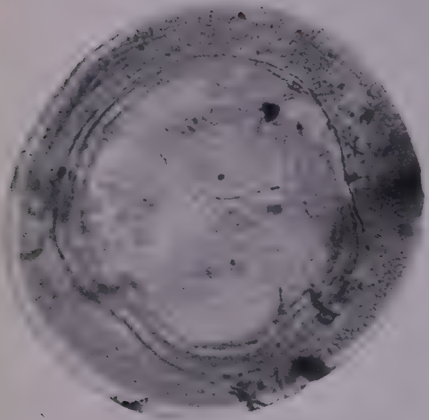

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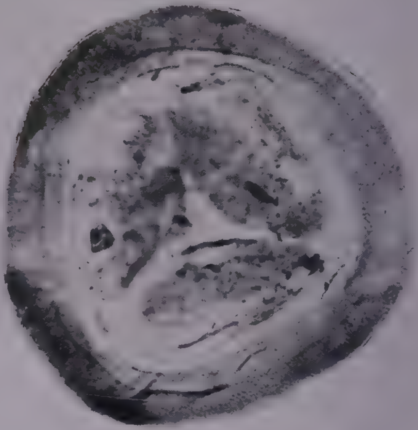

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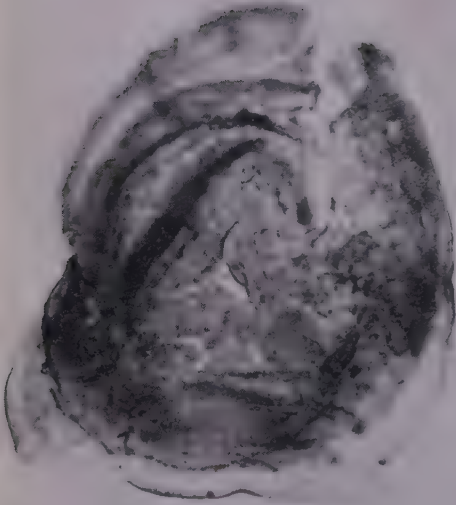

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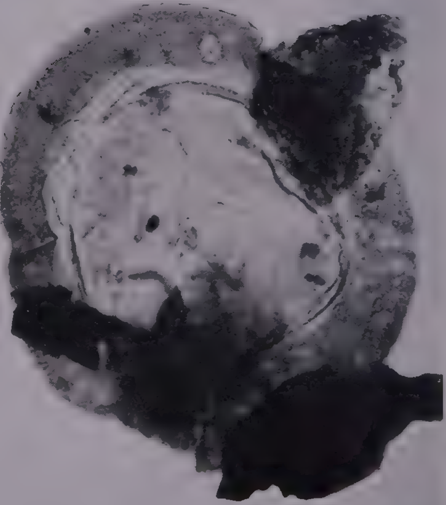

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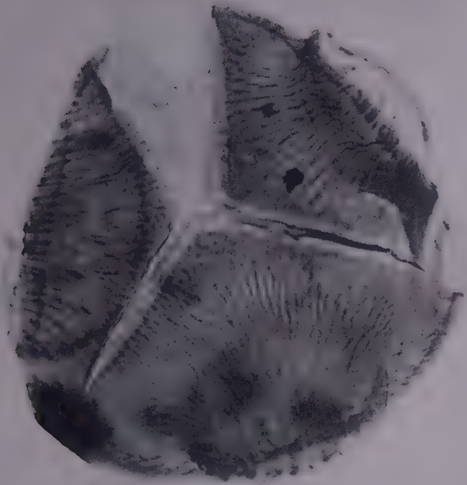

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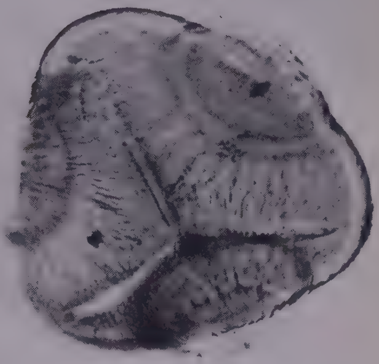

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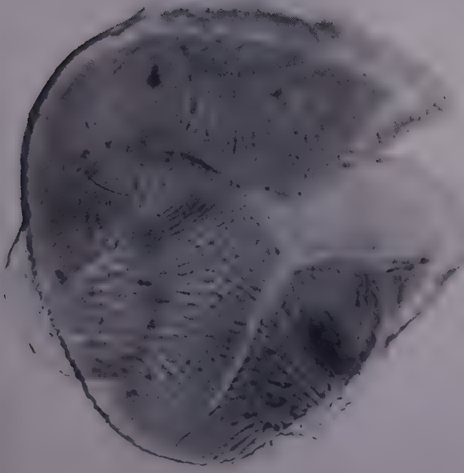

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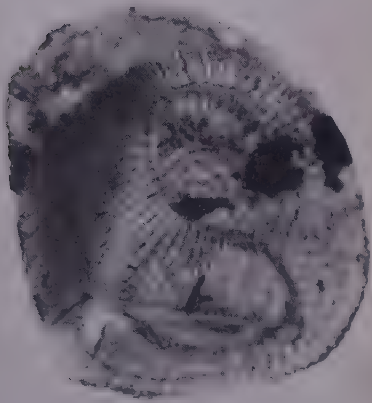

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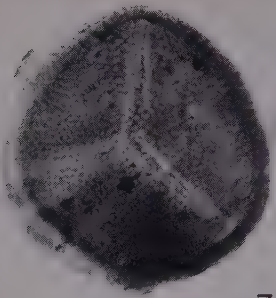
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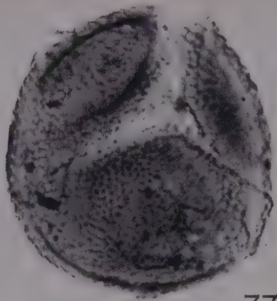
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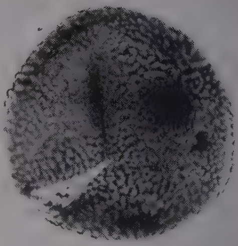
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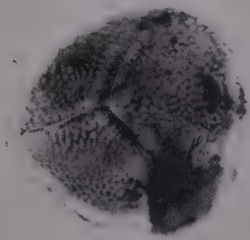
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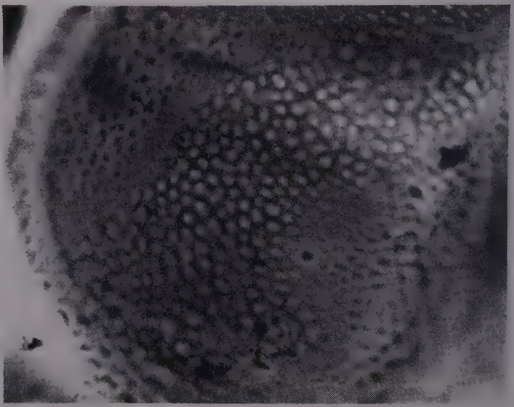
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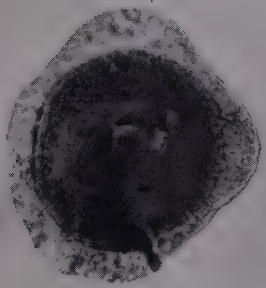
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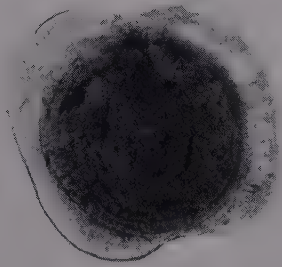
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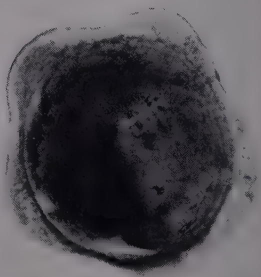
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THE GENUS *CODIUM* (CHLOROPHYTA) IN SOUTHERN AUSTRALIA

By P. C. Silva* and H. B. S. Womersley†

[*Manuscript received May* 9, 1956]

Summary

Fifteen species of *Codium*, five of which were previously undescribed, occur along the southern coast of Australia. Detailed descriptions and illustrations of all species are given, together with their distribution and notes on the habitat of each.

Introduction

The representation of *Codium* in Australia, like that of marine algae in general, is rich both in individuals and in species. The present systematic account treats those species found in the region between south-west Western Australia and the Victorian–New South Wales border, including Tasmania.

Specimens were made available for study from: University of Adelaide (AD); Herb. Agardh, Botaniska Museet, Lund (LD); Allan Hancock Foundation, University of Southern California (AHFH); British Museum (Natural History) (BM); Jardin Botanique de l'Etat, Bruxelles (BR); Botanical Museum, Copenhagen (C); Division of Plant Industry, C.S.I.R.O., Canberra (CANB); Royal Botanic Garden, Edinburgh (E); Chicago Natural History Museum (F); Instituto Botanico, Firenze (FI); Staatsinstitut für allgemeine Botanik, Hamburg (HBG); University of Tasmania, Hobart (HO); Royal Botanic Gardens, Kew (K); Rijksherbarium, Leiden (L); Botanische Staatssammlung, München (M); National Herbarium of Victoria, Melbourne (MEL); University of Michigan (MICH); National Herbarium of New South Wales, Sydney (NSW); New York Botanical Garden (NY); Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris (PC); State Herbarium of Western Australia, Perth (PERTH); Naturhistoriska Riksmusseet, Stockholm (S); Trinity College, Dublin (TCD); University of California, Berkeley (UC); United States National Museum (US); Victoria University College, Wellington (VUC).

Key to Species of Codium in Southern Australia

1. Thallus applanate or subglobose	2
1. Thallus erect, simple or dichotomously branched	8
2. Thallus applanate	3
2. Thallus subglobose	7
3. Utricles mostly less than 100 μ dia.	4
3. Utricles mostly greater than 100 μ dia.	6
4. Utricles devoid of hairs	1. *C. dimorphum*
4. Older utricles with hairs (or hair scars)	5
5. Utricles 600–1300 μ long, regularly and conspicuously capitulate, apices symmetrical	2. *C. capitulatum*

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† Department of Botany, University of Adelaide.

5. Utricles 435–800 (–1150) μ long, irregularly constricted below apex, apices asymmetrical .... 3. *C. lucasii*
  6. Utricles in small clusters, apical wall thickened into galeate cap to 56 μ thick .... 4. *C. perrinae*
  6. Utricles in large clusters, apical wall thin or moderately thickened (–32 μ) .... 5. *C. spongiosum*
7. Utricles mostly 450–1000 μ dia. at apex .... 6. *C. mamillosum*
7. Utricles mostly 90–125 μ dia. at apex .... 7. *C. pomoides*
  8. Thallus simple or once-divided, broad and flat, felt-like .... 8. *C. laminarioides*
  8. Thallus dichotomously branched, branches terete or somewhat complanate 9
9. Utricles not mucronate 10
9. Utricles mucronate 14
  10. Utricles often longer than 1 mm 11
  10. Utricles never as long as 1 mm 12
11. Utricles with galeate thickening at apex .... 9. *C. galeatum*
11. Utricles with thin or slightly thickened apical wall, not galeate .... 10. *C. duthieae*
  12. Medullary filaments with plugs close to point of departure from utricle .... 11. *C. harveyi*
  12. Medullary filaments with plugs conspicuously distant from point of departure from utricle 13
13. Utricles prominently introrsely umbonate .... 12. *C. muelleri*
13. Utricles not introrsely umbonate .... 13. *C. australicum*
  14. Utricles mostly longer than 1 mm .... 14. *C. fragile*
  14. Utricles 475–680 μ long .... 15. *C. spinescens*

1. **Codium dimorphum** Svedelius, Svenska Exped. Magellansländerna 3(8): 300, pl. 16, fig. 1; pl. 17, figs. 16–19 (1900).

Fig. 1

Codium adhaerens C. Agardh var. *incrassatum* Dellow, Trans. Roy. Soc. N.Z. **80**: 124, figs. 8, 9 (1952).

Thallus applano-pulvinate, 2·5–10 mm thick, to 10 cm dia., tending to be crescent-shaped, lobed at margins, very firm, dark green. Utricles in large clusters, cylindrical (47–) 55–80 (–90) μ dia., 550–1000 μ from apex to point of origin from parent utricle; apices rounded to subtruncate; utricular wall 1·5 μ thick, at apex slightly thickened, apical thickening tending to make apex truncate or depressed. Utricles from free edge of thallus with marked apical thickening (–30 μ), expanded below apex (–125 μ dia.); incrassate apices lamellate, internally alveolate, and externally often foveolate. Hairs absent. Medullary filaments originating singly at base of each new utricle by broad outgrowth so that filament and utricle intergrade, gradually tapering to 20–35 μ dia. Gametangia narrowly ellipsoid to cylindrical, 44–75 μ dia., 240–380 μ long, borne singly on very short pedicel (about 3 μ long) 370–480 μ below apex of utricle.

Type.—Melinca, Guaitecas Is., Chile, *P. Dusen* (Herb. Svedelius; fragment in UC).

Known Range.—Tasmania. New Zealand. Chatham Is. Chile.

Representative Specimens Examined.—TASMANIA: Port Arthur, exposed positions in sublittoral fringe, 26.i.1951, *Cribb* 117·5 (UC). Cape Forestier, 21.vi.1954, *I. Bennett* (AD, A19,830). Tasman I., 28.vi.1954, *I. Bennett* (AD, A19,831). NEW ZEALAND: Stewart I.: Half Moon Bay, 25.ii.1935, *L. M. Jones*, Tilden's South Pacific Plants, ser. 2, no. 753 (F). Otago: St. Clair, Dunedin, 23.vi.1951, *M. Naylor* (VUC). Canterbury: Banks Peninsula, *S. Berggren* (LD). CHATHAM ISLANDS: *Travers* 40 (LD).

The distribution of this species undoubtedly is related to the Antarctic Circumpolar Current, which has its biological counterpart in an antarctic circumpolar marine algal province. It is apparently restricted to the sublittoral fringe or lower littoral zones in south-east Tasmania.

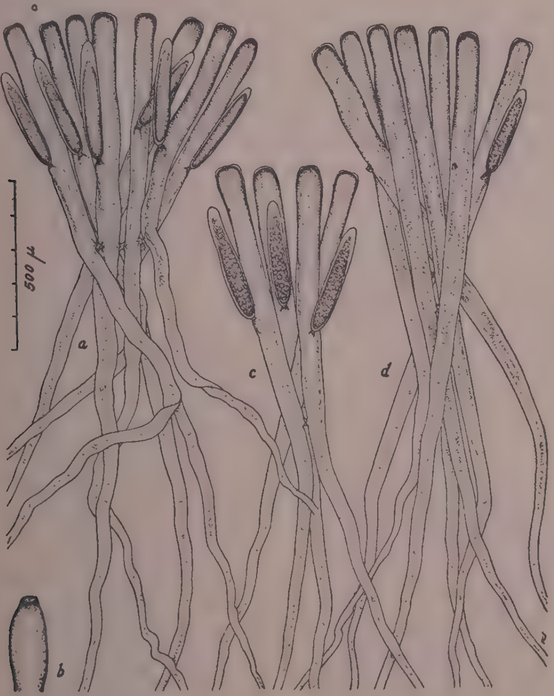

Fig. 1.—*C. dimorphum*. *a, b* (Melinca, Chile, *Dusen* = type). *a*, mature group of utricles from centre of thallus; *b*, apex of utricle from edge of thallus, showing marked thickening; *c*, (St. Clair, Dunedin, New Zealand, *Naylor*) mature group of utricles from centre of thallus; *d*, (Port Arthur, Tas., *Cribb* 117·5) mature group of utricles from centre of thallus.

2. **Codium capitulatum** sp. nov.

Fig. 2; Plate 1, Fig. 1

Thallus applanatus, cum forma extenta et irregulare, adhaerens firmiter substrata, ad marginem cum lobosis, ad 1 cm crassus, firmus, fusco-viridis. Utriculi in magnis fasciculis, cylindrici; utriculi primi 600–1300 μ long., 70–140 μ dia. ad apicem, ad 230 μ dia. in partem mediam, constricti 50–80 μ infra apicem, cum multo pilorum cicatricibus in zona 95–270 μ infra apicem, interdum in verticalibus ordinibus; utriculi secondarii 600–1000 μ long., 40–85 μ dia. ad apicem, distincte constricti 50–80 μ infra apicem, cum forma capitata, ad 115 μ dia. infra constrictionem, interdum cum multos pilorum cicatricibus, ordinatis similiter ad utriculos primos; apices rotundata symmetricaliter; membrana utricularis 1–1·5 μ crass., ad apicem paululum incrassata (2–4 μ in utriculis majoribus natu). Filamenta medullaria plerumque 16–45 μ dia. Gametangia fusiformia, 60–110 μ dia., 240–380 μ long., 1 gametangium per utriculum in brevi pediculo positum (*c.* 7 μ long.), 320–415 μ infra apicem (ad aut ferme super partem mediam).

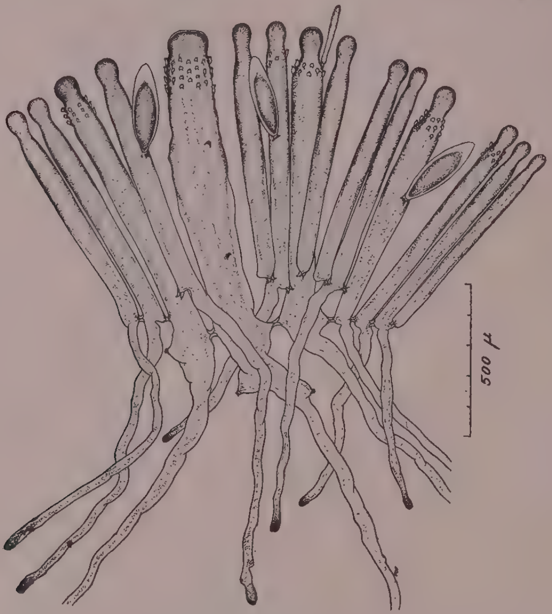

Fig. 2.—*C. capitulatum* (Elliston, S.A., *Womersley* (AD, A13,623)). Mature group of utricles from centre of thallus.

Thallus applanate, of extended and irregular shape, closely adherent to rock, with marginal lobes, to 1 cm thick, firm, dark green. Utricles in large clusters, cylindrical; primary utricles 600–1300 μ long, 70–140 μ dia. at apex, expanding to 230 μ dia. in middle, constricted 50–80 μ below apex, with numerous hair scars in band 95–270 μ below apex, at times arranged in vertical rows; secondary utricles 600–1000 μ long, 40–85 μ dia. at apex, prominently constricted 50–80 μ below apex, giving a capitate appearance, expanding to 115 μ dia. below constriction, often with numerous hair scars arranged as in primary utricles; apices symmetrically rounded; utricular wall thin (1–1·5 μ), very slightly thickened at apex (2–4 μ in older utricles). Medullary filaments mostly 16–45 μ dia. Gametangia fusiform, 60–110 μ dia., 240–380 μ long, borne 1 per utricle on short pedicel (about 7 μ long), 320–415 μ below apex (at or just above middle).

Type.—Elliston, west coast of Eyre Peninsula, S.A. (lower littoral inside bay), 14.ii.1954, *Womersley* (AD, A19,384). Isotypes in BM, L, LD, MEL, UC.

Other Specimens Examined.—SOUTH AUSTRALIA: Point Sinclair, lower littoral, 25.i.1951, *Womersley*, (AD, A15,188). Point Sinclair, uppermost sublittoral in pools, 8.ii.1954, *Womersley* (AD, A19,558). Elliston, lower littoral in bay, 15.i.1951, *Womersley* (AD, A16,623). Point Westall, upper sublittoral pools, 19.i.1951, *Womersley* (AD, A13,807). Port Willunga, upper sublittoral, 23.ii.1955, *E. Wollaston* (AD, A20,400). VICTORIA: Point Lonsdale, *Iona Maclennan* (UC). Walkerville, Waratah Bay, *I. Bennett*, Nov. 1949, lower littoral (AD, A15,236).

C. capitulatum is common just below and above low tide level on rock platforms on the west coast of Eyre Peninsula, especially where there is shade. Wave conditions vary from fairly calm to rough.

C. capitulatum is most closely related to *C. lucasii* on southern Australian coasts, from which it is easily distinguished, however, by its relatively long, regularly constricted utricles with symmetrically rounded apices. The utricles of *C. lucasii* by comparison are considerably shorter, not so regularly nor so conspicuously constricted, and with asymmetrical apices which may be rounded, truncate, or depressed. Moreover, unlike *C. capitulutum*, the apices of utricles of *C. lucasii* may be moderately to markedly incrassate with internal alveolation or cribrose pitting.

3. **Codium lucasii** Setchell in Lucas, Proc. Linn. Soc. N.S.W. **60**: 200, text-fig. 3 (1935). Lucas, Seaweeds S. Aust. pt. **1**: 50, fig 31 (1936). May, Proc. Linn. Soc. N.S.W. **63**: 212 (1938). Womersley, Trans. Roy. Soc. S. Aust. **73**: 145 (1950). Silva, Univ. Calif. Publ. Bot. **25**: 87, 92–94, fig. 11 (1951). Guiler, Pap. Roy. Soc. Tasm. **86**: 75 (1952).

Fig. 3

Thallus applanate or pulvinate, firm, slippery, dark green, 2·5–8 mm thick, at first orbicular, soon giving off broad or narrow lobes which form a close flat pattern rather tightly adherent to substratum but with free margins. Utricles in large clusters, cylindrical (45–) 50–100 (–130) μ dia. at apex, 435–800 (–1150) μ long, slightly to markedly constricted 40–70 μ below apex; apices truncate, depressed, or rounded, usually not perfectly symmetrical; utricular wall thin (1 μ), at apices slightly to moderately or even markedly thickened (–65 μ), internally often shallowly alveolate to deeply cribrosely pitted; hairs (or hair scars) common on older utricles, forming band of one or more irregular whorls extending from 70 to 145 μ below apex of utricle. Medullary filaments mostly 13–33 μ dia. Gametangia fusiform to oblance-ovoid, 60–125 μ dia., 215–360 μ long, borne 1 per utricle on short pedicel, 280–360 μ below apex.

Type.—Bondi, N.S.W., Aug. 1901, *A. H. S. Lucas* (UC 395199).

Known Range.—Cottesloe, W.A., around southern Australia to Redcliffe, Qld.

Representative Specimens Examined.—WESTERN AUSTRALIA: Cottesloe, 12.vi.1951, cast ashore, *Royce* 1039 (PERTH, UC). SOUTH AUSTRALIA: Head of Great Australian Bight, lower littoral, 4.ii.1954, *Womersley* (AD, A19,149). Elliston, lower littoral, 15.i.1951, *Womersley* (AD, A20,401) (UC). Pennington Bay, Kangaroo I., upper sublittoral reef pools, 28.i.1944, *Womersley* (AD, A2268). VICTORIA: Sorrento, upper sublittoral pools in shaded cave, 2.vi.1953, *Womersley* (AD, A18,830). NEW SOUTH WALES: Maroubra Bay, Oct. 1931, *A. H. S. Lucas* (UC). Balmoral, Sydney Harbour, 30.iv.1950, *Cribb* 50·9 (UC). Port Jackson, *W. H. Harvey*, Algae Australicae Exsiccatae 576, sub. *C. adhaerens* (TCD). Narrabeen Head, 20.iv.1951, *May* 2821 (NSW, UC). Newcastle, *W. H. Harvey*, Algae Australicae Exsiccatae 576, sub. *C. adhaerens*

(K). Fingal, 10.iv.1949, *Cribb* 12·5 (UC). QUEENSLAND: Redcliffe, 9.vii.1949, *Cribb* 20·16 (UC).

C. lucasii occurs just below or above low tide level, under moderate to rough wave action.

The applanate species of Australian *Codium* prior to the publication of *C. lucasii* were referred to *C. adhaerens* C. Agardh, which is strictly European in distribution. Plants of *C. lucasii* from Port Jackson and Newcastle were distributed by Harvey as Algae Australicae Exsiccatae 576 and are the bases of the following erroneous records of *C. adhaerens*: Harvey 1863, p. lviii; Sonder 1880, p. 38; Lucas 1912, p. 171; May 1938, p. 212.

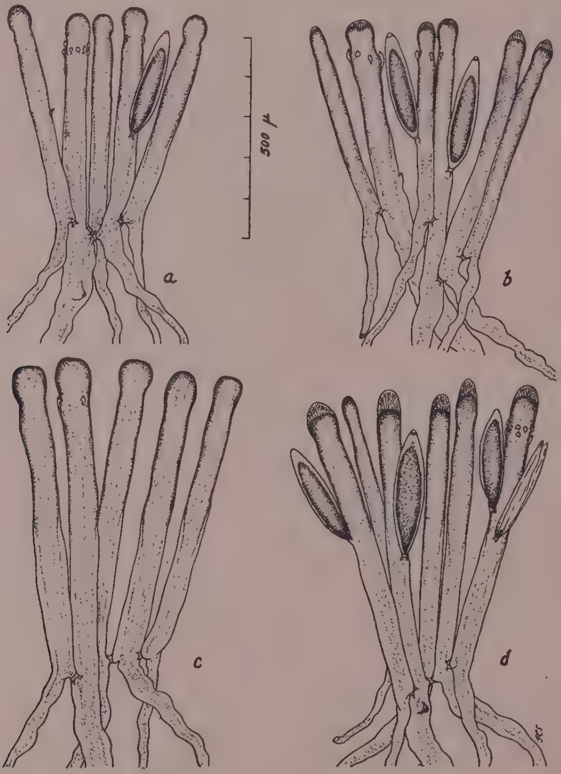

Fig. 3.—*C. lucasii*. Mature groups of utricles from centre of thallus. *a*, Redcliffe, Qld., *Cribb* 20·16; *b*, Balmoral, Sydney Harbour, N.S.W., *Cribb* 50·9; *c*, Elliston, S.A., *Womersley* (AD, A20,401); *d*, Cottesloe, W.A., *Royce* 1039.

There is some doubt whether the Lord Howe Island record of Lucas (1935) should be referred to *C. lucasii*.

C. lucasii is closely related to, if not identical with, a widely distributed form in South Africa.

4. **Codium perrinae** Lucas, Proc. Linn. Soc. N.S.W. **60**: 203, text-fig. 4 (1935). Womersley, Trans. Roy. Soc. S. Aust. **73**: 145 (1950). Guiler, Pap. Roy. Soc. Tasm. **86**: 75 (1952).

Fig. 4

Thallus pulvinate, orbicular when young, becoming crescentic or annular, to 12 cm across, glaucous green. Utricles in small clusters, ellipsoid-cylindrical to slightly clavate, 130–240 μ dia. at apex, to 375 μ dia. at distance of 230–350 μ below apex, 920–1700 μ long; apical wall moderately to markedly thickened into a lamellate galeate cap to 56 μ thick, occasionally slightly introrsely umbonate, externally foveolate. Medullary filaments mostly 26–60 μ dia. Hairs absent. Gametangia fusiform to subcylindrical, 65–100 μ dia., 370–450 μ long, borne 1 or 2 per utricle on a short pedicel 540–630 μ below apex of utricle.

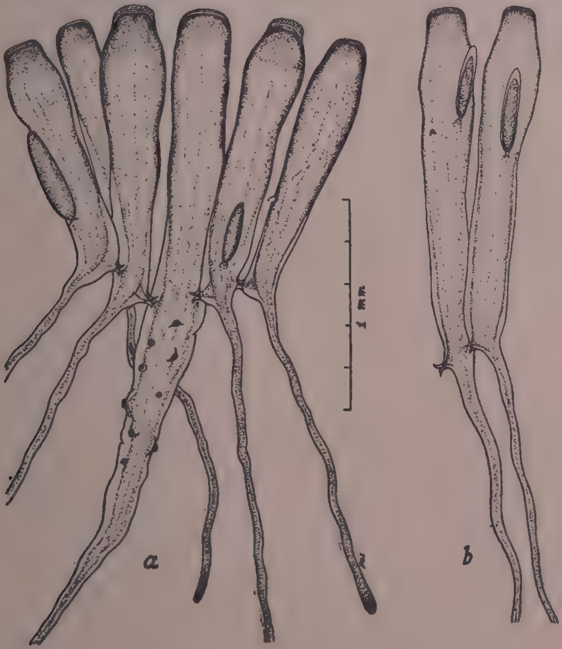

Fig. 4.—*C. perrinae.* *a*, (D'Estrees Bay, Kangaroo I., S.A., *Womersley* (AD, A12,781)); mature group of utricles with two juveniles arising as buds; *b*, (Nora Creina, S.A., *Womersley* (AD, A20,014)) group of utricles with gametangia.

Type.—Low Head, Bass Strait, Tas., Jan. 1930. *F. Perrin & A. H. S. Lucas* (CANB).

Known Range.—From Stenhouse Bay, Yorke Peninsula, to Low Head in Tasmania (see below).

Other Specimens Examined.—SOUTH AUSTRALIA: Stenhouse Bay, Yorke Peninsula, drift, 9.iv.1950, *Womersley* (AD, A13,168). D'Estrees Bay, Kangaroo I., upper sublittoral reef pools, 11.i.1950, *Womersley* (AD, A12,781) (BM, UC). Lefebre Peninsula, *F. von. Mueller* (HBG). Nora Creina, upper sublittoral pool, 14.xi.1955, *Womersley* (AD, A20,014). TASMANIA: Low Head, Jan. 1930, *Perrin & Lucas* (UC). Bellerive, June 1909, *Rodway* (HO).

Guiler (1952, p. 75) has reported several specimens from Tasmania under the name *Codium bursa* (L.) C. Agardh, a species restricted to warm Atlantic waters. That from Bellerive is *C. perrinae*; the others have not been checked, but may be *C. pomoides*.

C. perrinae is not a common species, but probably more general in occurrence than the known localities would indicate. It occurs in reef pools and the upper sublittoral zone under moderately rough conditions.

5. **Codium spongiosum** Harvey, Trans. R. Irish Acad. **22**: 565 (1855); Harvey, Phyc. Austral. **1**: pl. 55 (1858); **5**: lvii (1863). Sonder, Fragm. Phytogr. Aust. **11** (suppl.): 38 (1880). J. Agardh, Acta Univ. Lund. **23**: 38 (1887). De Toni, Syll. Alg. **1**: 489 (1889). Wilson, Proc. Roy. Soc. Vict. **4**: 188 (1892). J. Agardh, Acta Univ. Lund. **29**: 99 (1894). Lucas, Proc. Linn. Soc. N.S.W. **37**: 171 (1912). Schmidt, Bibl. Bot., Stuttgart **23** (Hft. 91): 32, figs. 14, 15? (1923). Lucas, Proc. Linn. Soc. N.S.W. **60**: 202 (1935); Seaweeds S. Aust. 1: 51 (fig. 32) (1936). May, Proc. Linn. Soc. N.S.W. **63**: 212 (1938). Womersley, Trans. Roy. Soc. S. Aust. **71**: 247 (1947); ibid. **72**: 161 (1948); ibid. **73**: 146 (1950). May, Proc. Linn. Soc. N.S.W. **76**: 92 (1951). Guiler, Pap. Roy. Soc. Tasm. **86**: 75 (1952).

Fig. 5

Thallus pulvinate or applanate, with undulate to cerebriform lobes, spongy, to 15 cm thick, to 20 (–50) cm dia., loosely adherent to substratum. Utricles in large clusters, younger utricles cylindrical or clavate, 130–390 μ dia., 1·5–4 (–6) mm long, older utricles to 520 μ dia. at apex, gradually enlarging below up to 850 μ dia.; apices subtruncate to rounded; utricular wall 2–3 μ thick, at apices very slightly to moderately thickened (–32 μ), incrassate apices finally lamellate and slightly introrsely umbonate. Hairs (or hair scars) abundant, forming band about 120–200 μ wide and 130–430 μ below apex of utricle. Medullary filaments mostly 30–100 μ dia. Gametangia lance-ovoid or ampulliform, 50–175 μ dia., 215–360 μ long, usually several per utricle, each borne on short pedicel 360–660 μ below apex of utricle.

Lectotype.—King George's Sound, W.A., *W. H. Harvey*, Algae Australicae Exsiccatae 577 (TCD).

Known Range.—Point Cloates, W.A., around southern Australia to Green I. (near Cairns), Qld.; Tasmania. South Africa. Mauritius. Lord Howe I. New Caledonia. Hawaiian Is.

Representative Specimens Examined.—WESTERN AUSTRALIA: Point Cloates, comm. *May* 2822 (UC). Fremantle, 10.iv.1952, *Royce* 1158 (UC). Thompson Bay, Rottnest I., 19.x.1934, *C. M. Crosby*, Tilden's South Pacific Plants, ser. 2, no. 79 (F). King George's Sound, *W. H. Harvey*, Algae Australicae Exsiccatae 577 (K, TCD). SOUTH AUSTRALIA: Elliston, west coast of Eyre Peninsula, 15.i.1951, *Womersley* (AD, A16,625) (BM, K). Coffin Bay, upper sublittoral, 10.i.1951, *Womersley*, (AD, A13,751). Pig I., Pelican Lagoon, Kangaroo I., upper sublittoral, 12.iv.1947, *Womersley* (AD, A4489) (F, UC). Rocky Point Beach, Kangaroo I., drift, 4.vi.1947, *Womersley* (AD, A5706) (L). Port Vincent, drift, 8.iv.1950, *Womersley* (AD, A13,129). VICTORIA: Hayling's Reef, Apollo Bay, 17.i.1949, *Pope & Bennett* (AD, A15,276). NEW SOUTH WALES: Port Jackson, Feb.–Mar. 1881, dredged from 0·5 fm by H.M.S. *Alert*, *Coffinger* (BM). Middle Harbour, May 1906, *A. H. S. Lucas* (UC). Lake Macquarie, Jan. 1918, *A. H. S. Lucas* (NSW). QUEENSLAND: Moreton Bay, Jan. 1912, *C. T. White* (K). Point Lookout, Stradbroke I., Sept. 1949, *Cribb* 113 (UC). Bowen, *A. H. S. Lucas* (UC). Green I., near Cairns, June 1931, *Perrin & Lucas* (UC). TASMANIA: Stanley, *F. von Mueller* (K).

C. spongiosum is probably the most common prostrate *Codium* in southern Australia, being common under relatively calm conditions—such as the Gulf region of South Australia. It is a sublittoral species, extending to just below low tide level.

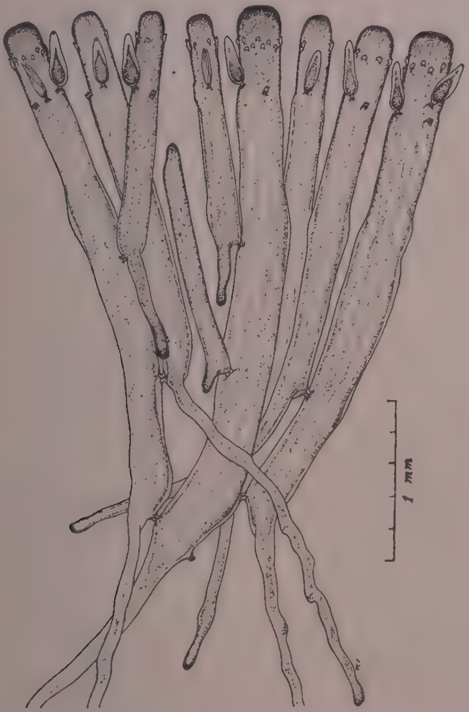

Fig. 5.—*C. spongiosum* (Point Lookout, Stradbroke I., Qld., *Cribb* 113). Mature group of utricles.

6. **Codium mamillosum** Harvey, Trans. R. Irish. Acad. **22**: 565 (1855); Phyc. Austral. **1**: pl. 41 (1858); Phyc. Austral. **5**: lvii (1863). Sonder, Fragm. Phytogr. Aust. **11** (suppl.): 38 (1880). J. Agardh, Acta Univ. Lund. **23**: 39 (1887). De Toni, Syll. Alg. **1**: 491 (1889). Lucas, Proc. Linn. Soc. N.S.W. **37**: 171 (1912); ibid. **52**: 558 (1927); Trans. Roy. Soc. S. Aust. **53**: 46 (1929*b*); Seaweeds S. Aust. **1**: 53, fig. 34 (1936). Womersley, Trans. Roy. Soc. S. Aust. **71**: 244 (1947); ibid. **72**: 161 (1948); ibid. **73**: 145 (1950); Rep. Aust. Geogr. Soc. No. **1** (3B): 36 (1953).

Fig. 6

Codium mamillosum var. *typicum* O. C. Schmidt, Bibl. Bot., Stuttgart **23** (Heft 91): 37, fig. 19 (1923).

Codium bursa var. *australis* Sonder, Linnaea **25**(6): 660 (1853).

Thallus glaucous green, more or less globose, to 7 cm dia., attached to substratum by tuft of rhizoidal holdfasts. Utricles in small clusters, clavate, subtruncate or slightly rounded at apex, (400–) 450–1000 μ dia. at apex, often expanded below apex (–1500 μ dia.), tapering toward base (3–) 4–7 (–9) mm long, 5·5–13 × long as broad; utricular wall 2·5–5 μ thick, slightly to moderately thickened at apex (–40 μ), incrassate apices finely lamellate. Hairs absent. Medullary filaments mostly 40–105 μ dia., several arising by slender outgrowths from base of each utricle, often branched or constricted near origin or both. Gametangia narrowly ellipsoid, ovoid, or ampulliform, 130–250 μ dia. (390–) 520–780 μ long, 1–3 per utricle, each borne on short pedicel (about 10 μ long) 1–2 mm below apex.

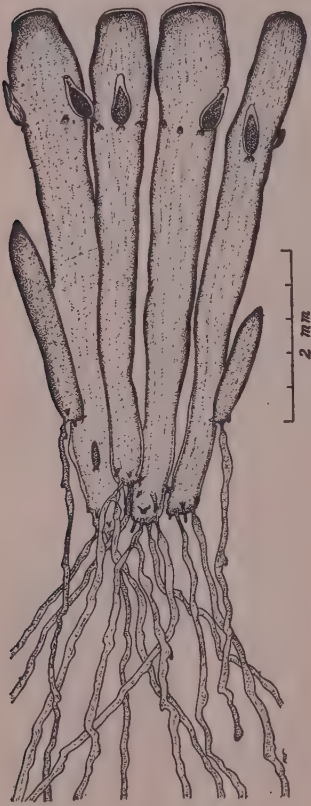

Fig. 6

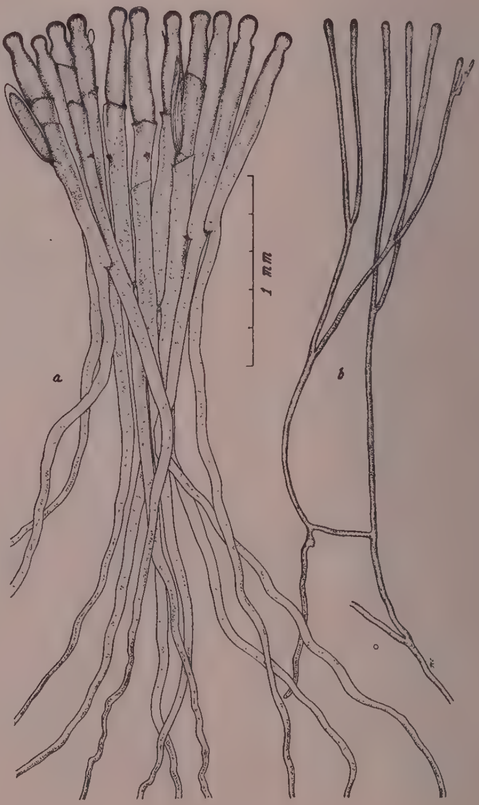

Fig. 7

Fig. 6.—*C. mamillosum* (City Beach, Perth, W.A., *Royce* 1200). Mature group of utricles.

Fig. 7.—*C. pomoides* (Mouth of Currie River, Tas., *Cribb* 75·16). *a*, mature group of utricles; *b*, juvenile utricle system.

Lectotype.—Swan River, W.A., *W. H. Harvey*, Algae Australicae Exsiccatae 578 (TCD).

Known Range.—City Beach, Perth, to Warrnambool, Vic. Hawaiian Is.

Representative Specimens Examined.—WESTERN AUSTRALIA: City Beach, Perth, 7.v.1952, *Royce* 1200 (PERTH, UC). Cottesloe, Aug. 1928, *A. H. S. Lucas* (NSW). Rottnest I., 10.viii.1950, *Cribb* 67·1 (UC). Fremantle, *W. H. Harvey*, Algae Australicae Exsiccatae 578 (C, HBG, K, L, MEL, NSW, NY, PC, TCD, US). Esperance Beach, 2.ix.1947, *J. H. Willis* (MEL). Recherche Archipelago, 20.xi.1950, *J. H. Willis* (AD, A15,848). SOUTH AUSTRALIA: Elliston, low littoral in bay, shaded, 15.i.1951, *Womersley* (AD, A16,622) (K, UC). Holdfast Bay, July, 1943, *J. R. Harris* (AD, A1797) (UC). Lefebre Peninsula, July 1852, *F. von Mueller* (MEL). Victor Harbour, 21.viii.1946, *May* 2265 (UC). West Beach, 12.ix.1948, *Womersley* (AD, A8760) (F, L, UC). Rocky Point Beach, Kangaroo I., 26.viii.1950, *Womersley* (AD, A13,361) (BM). Pennington Bay, Kangaroo I., drift, 23.i.1944, *Womersley* (AD, A2265). VICTORIA: Warrnambool, Jan. 1927, *A. H. S. Lucas* (UC).

C. mamillosum is a common species within its range, especially in calmer localities. It is a sublittoral species, only rarely reaching to low tide level in shaded habitats.

C. bursa var. *australis* Sonder is referable to *C. mamillosum*, judging from an examination of the type specimen (Lefebre Peninsula, *F. von Mueller*, MEL). However, the plant distributed under this name by Harvey as Algae Australicae Exsiccatae 575 is *C. pomoides*. The following records of *C. bursa* are therefore based on both *C. mamillosum* and *C. pomoides*: Harvey 1863, pl. lviii; Sonder 1880, p. 38; Lucas 1912, p. 171.

Close relatives of *C. mamillosum*, namely, *C. globosum* Lucas and *C. cranwelliae* Setchell, are found in Queensland and New Zealand respectively.

7. **Codium pomoides** J. Agardh, Acta Univ. Lund. **29** (Afd. 2, Nr. 9): 100 (1894). Wilson, Proc. Roy. Soc. Vict. **4**: 188 (1892) (nomen nudum). Schmidt, Bibl. Bot., Stuttgart **23** (Heft 91): 36 (1923). Svedelius, Ark. Bot. **19**(3): 56, fig. 13 (1924). Lucas, Seaweeds S. Aust. **1**: 53, fig. 33 (1936). Womersley, Trans. Roy. Soc. S. Aust. **71**: 244, 247 (1947); ibid. **72**: 159, 161 (1948); ibid. **73**: 146 (1950).

Fig. 7

Thallus globose or subglobose, to 12 cm dia., very firm, solid when young, becoming hollow by attenuation of plexus of medullary filaments, attached to substratum by small tuft of rhizoidal holdfasts. Utricles in large clusters, subcylindrical (69–) 90–125 (–175) μ dia. at apex, expanding to maximum dia. of 200 μ about 350–700 μ below apex, 1–3 mm from apex to point of origin from parent utricle; apices symmetrically rounded; utricular wall 2·5–5 μ thick, at apex usually slightly thickened, at times moderately thickened (–32 μ), lamellate, with a slight introrse umbo which is faintly alveolate. Utricles adjacent to base clavate or fusiform, not capitate, larger than those from other parts of thallus, 140–280 μ dia. Juvenile utricle systems abundant in all parts of thallus, intermixed with mature utricle clusters, especially abundant in basal region. Typical hairs absent, but scars from anomalous outgrowths common. Gametangia narrowly ellipsoid to cylindrical, 55–95 μ dia., 400–510 μ long, borne singly on pedicel about 10 μ long 625–700 μ below apex of utricle.

Type.—"Hab. ad oras australes Novae Hollandiae; legit J. Br. Wilson". The specimen should be in Herb. Agardh but it has not been located.

Known Range.—From 10 miles east of Eucla (W.A.–S.A. border) to Walkerville, Vic.; Tasmania.

Representative Specimens Examined.—SOUTH AUSTRALIA: 10 miles east of Eucla, drift, 3.ii.1954, *Womersley* (AD, A19,241). Elliston, upper sublittoral, 15.i.1951, *Womersley* (AD, A13,621) (BM, K). West Beach, 12.ix.1948, *Womersley* (AD, A8759) (F, L, UC). Rocky Point Beach, Kangaroo I., drift, 4.vi.1947, *Womersley* (AD, A5705). Pennington Bay, Kangaroo I., upper sublittoral, 28.i.1944, *Womersley* (AD, A2267). VICTORIA: Port Fairy, *W. H. Harvey*, Algae Australicae Exsiccatae 575, sub. *C. bursa*? var. *australis* (LD, BM, K, MEL, NSW, PC). Point Lonsdale, *Iona Maclennan* (UC). TASMANIA: Hunter I., N.W. Tas., upper sublittoral, 14.i.1954, *I. Bennett* (AD, A19,667). Low Head, Jan. 1930, *Perrin & Lucas* (UC). Mouth of Currie River, 17.ix.1950, drift, *Cribb* 75·16 (UC). Barnes Bay, Bruny I. 4–6 fm, 15.i.1949, *Womersley* (AD, A10,174).

C. pomoides is found mainly in the sublittoral fringe or upper sublittoral zone on rough coasts but also extends into deeper water. The thalli adhere very tightly to their substratum.

C. pomoides is one of the most interesting species of the genus anatomically and phylogenetically. Its only close relative is the highly restricted *C. johnstonei* Silva (1951) from deep waters of southern California and adjacent Baja California, Mexico.

Juvenile utricle systems are found abundantly throughout the thallus. An unmistakable ontogenetic series leading from a juvenile utricle system to a cluster of mature utricles has not yet been observed, but it seems probable that only certain of the juvenile utricles reach full size, the others shrivelling and falling off, thus accounting for the conspicuous scars to be seen on mature utricles.

Although typical hairs are not produced, in the region just below the constriction of the utricle (where hairs might be expected to develop) there are fairly numerous irregular outgrowths which shrivel and fall, leaving scars.

The following erroneous records of *C. bursa* are probably based at least in part on *C. pomoides*: Harvey 1863, p. lviii; Sonder 1880, p. 38; Wilson 1892, p. 187; Lucas 1912, p. 171; Lucas 1913, p. 59; Lucas 1929*a*, p. 10; Lucas 1929*b*, p. 46; Guiler 1952, p. 75.

8. **Codium laminarioides** Harvey, Trans. R. Irish Acad. **22**: 565 (1855). Harvey, Phyc. Austral. **5**: lvii (1863). Sonder, Frag. Phytogr. Aust. **11** (suppl.): 38 (1880). J. Agardh, Acta Univ. Lund. **23**: 47 (1887). De Toni, Syll. Alg. **1**: 497 (1889). Lucas, Proc. Linn. Soc. N.S.W. **37**: 171 (1912). Schmidt, Bibl. Bot., Stuttgart **23** (Heft 91): 59 (1923) (excluding South African record and fig. 42).

Fig. 8

Thallus comprising a short terete stipe (to 12 mm long) and a felt-like, flat, greatly expanded frond, 1·5–2 mm thick, to 80 cm broad, simple or once dichotomous, the two segments unequally developed and irregularly lobed. Utricles narrowly ellipsoid to cylindrical, mostly 4–7 × long as broad, 65–185 (–290) μ max. dia. (usually well below apex), 475–790 μ long; apices rounded, utricular wall 1·5–2 μ thick, at apex usually incrassate (–30 µ), conspicuously lamellate, occasionally faintly alveolate. Hairs (or hair scars) common, usually on all but youngest utricles, several (to 8) in irregular zone 70–150 µ below apex (where utricle is broadest). Medullary filaments mostly 20–55 µ dia. Gametangia cylindrical to lanciform, 40–86 µ dia., 175–245 µ long, 1–4 per utricle, each borne on short pedicel (about 5 µ long) on protuberance 310–420 µ below apex (near middle).

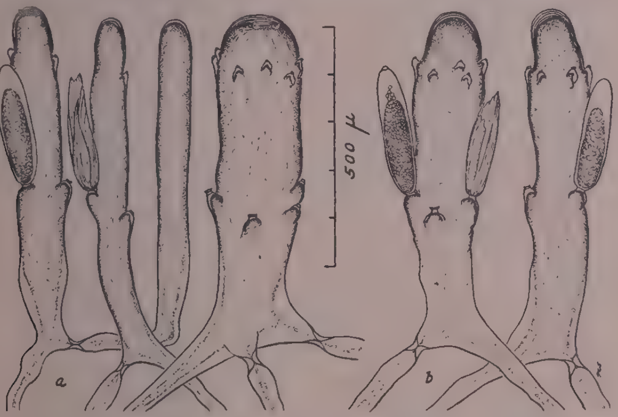

Fig. 8.—*C. laminarioides.* Individual utricles. *a*, Rottnest I., W.A., *Cribb* 61·42; *b*, Rottnest I., W.A., *Harvey* (NSW).

Lectotype.—Rottnest I., *W. H. Harvey*, Algae Australicae Exsiccatae 574 (TCD).

Known Range.—Cottesloe to King George's Sound, W.A.

Representative Specimens Examined—WESTERN AUSTRALIA: Rottnest I., *W. H. Harvey*, Algae Australicae Exsiccatae 574 (TCD); 10.viii.1950, *Cribb* 61·42 (UC). Cottesloe, Aug. 1928, *A. H. S. Lucas* (UC); 12.vi.1951, *Royce* 1040 (AD, PERTH); 15.vi.1952, *Royce* 1271 (PERTH, UC). Fremantle, *W. H. Harvey*, Algae Australicae Exsiccatae 574 (K, MEL, NSW, PC, US); Sept. 1854, *George Clifton* (BM).

C. laminarioides is apparently a deep water species, found cast up after winter storms.

This remarkable species has twice been reported erroneously from South Africa: by Barton (1893, p. 82) on the basis of a specimen collected by Boodle at Cape Point (BM), referable to *C. stephensiae* Dickinson; and by Schmidt (1923, p. 59), whose figure 42 undoubtedly was based on a Becker specimen from the Kowie, referable to *C. platylobium* Areschoug. *C. laminarioides* is closely related to both *C. platylobium* and *C. latum* Suringar (from Japan), from which it differs in habit by the almost complete suppression (or lack of development) of dichotomous branching.

9. **Codium galeatum** J. Agardh, Acta Univ. Lund. **23** (Afd. 3, Nr. 2): 42, pl. 1, fig. 1 (1887). De Toni, Syll. Alg. **1**: 494 (1889). Wilson, Proc. Roy. Soc. Vict. **4**: 187 (1892). Lucas, Proc. Linn. Soc. N.S.W. **37**: 171 (1912). Schmidt, Bibl. Bot., Stuttgart **23** (Heft 91): 45, fig. 27 (1923). Lucas, Sea-

weeds S. Aust. **1**: 54, fig. 35*a* (1936). Womersley, Trans. Roy. Soc. S. Aust. **71**: 244 (1947); ibid., **72**: 161 (1948); ibid. **73**: 145 (1950) (pro parte). Guiler, Pap. Roy. Soc. Tasm. **86**: 75 (1952).

Fig. 9

Codium tomentosum var. *australasiacum* Areschoug, Nova Acta Reg. Soc. Sc. Upsal. III, **1**: 368 (1854).

Thallus erect, to 100 cm high, regularly dichotomously branched, 5–15 often distant dichotomies, branches uniformly terete, not tapering towards tips, firm, 4–7 mm dia. Utricles stout, irregularly cylindrical to clavate (130–) 200–470 (–700) μ max. dia. (usually below apex), (650–) 750–1300 (–1500) μ long, usually 2–4 (–5) × long as broad; utricular wall 3 μ thick at base, becoming thicker toward apex, usually forming a conspicuously striated cap to 125 μ thick, sometimes scalariform. Hairs (or hair scars) occasional, when present one to few per utricle, borne at broadest part of utricle, 260–440 μ below apex. Medullary filaments mostly 33–80 (–115) μ dia., markedly constricted by plug at origin. Gametangia cylindrical to lance-ovoid, 57–185 μ dia., 275–530 μ long, 1 (rarely 2) per utricle, each borne on distinct pedicel (about 13 μ long) on protuberance below middle of utricle.

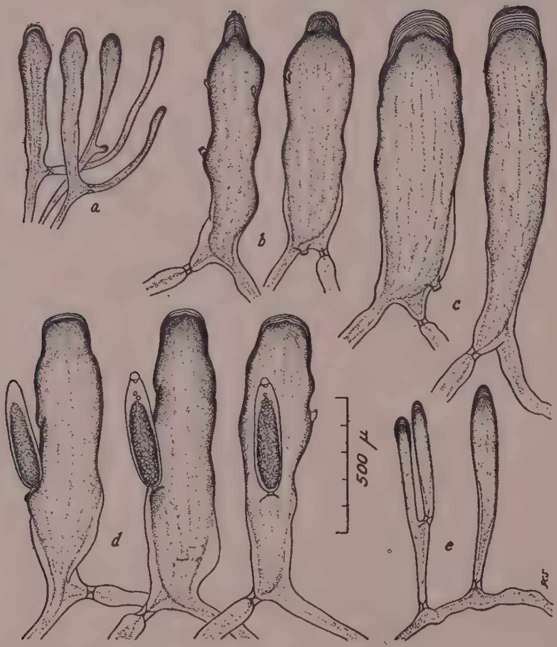

Fig. 9.—*C. galeatum*. *a*, *b*, *e*, Marino, Holdfast Bay, S.A., *Womersley*. (AD, A20,414) *a*, utricles from tip; *b*, utricles from middle of frond; *c*, (Port Phillip, Vic., *F. von Mueller*=lectotype) utricles from middle of frond; *d*, (City Beach, Perth, W.A., *Royce* 1196) utricles from middle of frond; *e*, utricles from base.

Lectotype.—Port Phillip, Vic., *F. von. Mueller* (LD, Herb. Agardh. 15588).

Known Range.—Champion Bay, W.A., around southern Australia to Ballina, N.S.W. (possibly to Rockingham Bay, Qld.).

Representative Specimens Examined.—WESTERN AUSTRALIA: Champion Bay, *Mrs. Gale* (MEL). City Beach, Perth, 7.v.1952, *Royce* 1196 (PERTH, UC). Rottnest I., 9.iv.1927, *W. A. Setchell* (UC); 9.viii.1950, *Cribb* 67·3 (UC). Geographe Bay, *F. von Mueller* (LD). Hamelin Bay, 21.vi.1950, *Royce* 713 (PERTH). King George's Sound, *W. H. Harvey*, Algae Australicae Exsiccatae 573, sub. *C. tomentosum*, (S, TCD); 1884, *F. von Mueller* (LD). Israelite Bay, 1888, *Miss Brooks* (MEL). Eucla, 1886, *T. D. Bath* (LD). SOUTH AUSTRALIA: Marino, Holdfast Bay, 21.v.1953, *Womersley* (UC). Elliston, upper sublittoral, 15.i.1951, *Womersley* (AD, A13,624). Vivonne Bay, Kangaroo I., shaded littoral pool, 4.i.1950, *Womersley* (AD, A12,752) (BM, K). Pennington Bay, Kangaroo I., drift, 14.i.1947, *Womersley* (AD, A4289) (MEL, UC). D'Estrees Bay, Kangaroo I., sublittoral fringe, 20.i.1947, *Womersley* (AD, A4151) (F). Port Elliot, drift, 17.x.1948, *Womersley* (AD, A9436) (S). Encounter Bay, Nov. 1929, *J. B. Cleland* (UC). Guichen Bay, 1.ix.1949, 5-8 fm, *Womersley* (AD, A10,936) (F). Rivoli Bay, Oct. 1848, *F. von Mueller* (MEL). VICTORIA: Bridgewater Bay, drift, 17.vii.1949, *C. Beauglehole* (AD, A12,034). Portland Bay, misit *Areschoug* (LD). Barwon Heads, Jan. 1903, *A. H. S. Lucas* (NSW). Port Phillip, *F. von Mueller* (LD, NY). Sorrento, 30.iv.1898, *H. T. Tisdall* (NSW). Walkerville, upper sublittoral, 19.v.1949, *Pope & Bennett* (AD, A12,203). NEW SOUTH WALES: Ballina, *Henderson* (MEL). QUEENSLAND: 1911, *Mrs. M. Doyle* (BM).

C. galeatum extends from the sublittoral fringe zone downwards on rough to moderate coasts. It is probably the commonest dichotomous species on rough coasts in South Australia and southern Western Australia.

C. tomentosum var. *australasiacum* Areschoug is referable to *C. galeatum*, judging from specimens in Herb. Areschoug (S), of which we consider as lectotype one labelled "*Codium tomentosum*. Victoria. Aresch".

10. **Codium duthieae** Silva, sp. nov.

Fig. 10; Plate 1, Fig. 2

Thallus erectus ad 60 cm alt., dichotome ramosus; rami omnino teretes, solum ad dichotomias aut fere omnino complanati; interdichotomiae 3–14 mm, dichotomiae ad 40 mm lat. Utricali cylindrici ad clavatos (130–) 175–500 (–720) μ dia. (450–) 670–1800 μ long.; apicibus late rotundatis, membrana utriculari 2–6 μ crass., ad apices (ad 42 μ) interdum incrassata. Pili (aut pilorum cicatrices) parci, interdum satis multi (ad 12 per utriculum), 185–430 μ infra apicem portati. Filamenta medullaria plerumque 43–72 μ dia. Gametangia lanceo-ovata, 70–160 μ dia. (235–) 270–430 μ long., aliquot (ad 8) per utriculum, omnia in pediculis *c.* 15 μ long. in protuberantia 345–675 μ infra apicem portata.

Thallus erect, to 60 cm high, dichotomously branched; branches wholly terete, flattened only at the dichotomies, or flattened almost throughout; interdichotomies 3–14 mm broad, dichotomies to 40 mm broad. Utricles cylindrical to clavate (130–) 175–500 (–720) μ dia., (450–) 670–1800 μ long; apices broadly rounded; utricular wall 2–6 μ thick, at apices occasionally thickened (to 42 μ). Hairs (or hair scars) occasional, at times fairly numerous (to 12 per utricle), borne 185–430 μ below apex. Medullary filaments mostly 43–72 μ dia. Gametangia lanceovoid, 70–160 μ dia. (235–) 270–430 μ long, several (to 8) per utricle, each borne on pedicel about 15 μ long on protuberance 345–675 μ below apex.

Type.—Cast ashore, Strandfontein, False Bay, Cape Province, South Africa, 13.xi.1935, *G. F. Papenfuss* 24 (UC 920260).

Known Range.—Champion Bay, W.A., to Western Port, Vic.; Currie River, Tas. Swakopmund, South West Africa, around the Cape of Good Hope to the mouth of the Limpopo River, Mozambique.

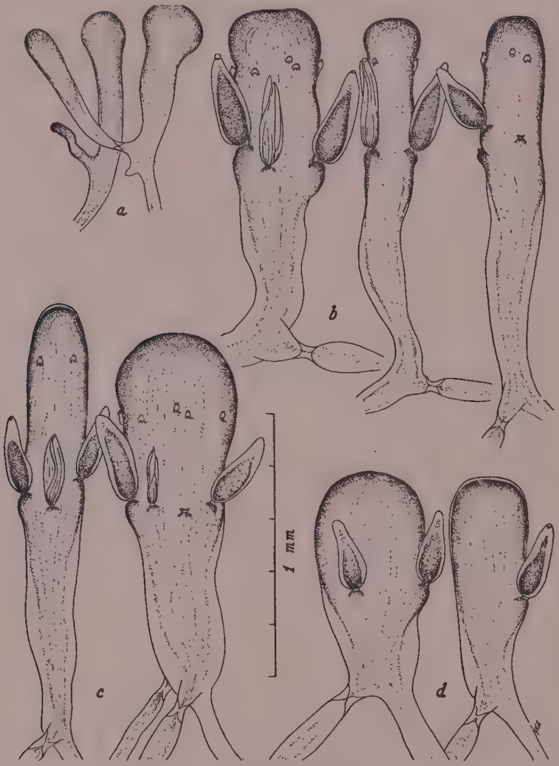

Fig. 10.—*C. duthieae*. *a*, *b*, Strandfontein, False Bay, Cape Province, South Africa, *Papenfuss* 24=type. *a*, utricles from tip; *b*, utricles from middle of frond; *c*, (Elliston, S.A., *Womersley* (AD, A16,624)) utricles from middle of frond; *d*, (Melkbosch, Cape Province, South Africa, *Papenfuss* 358) utricles from middle of frond.

Representative Australian Specimens Examined.—WESTERN AUSTRALIA: Champion Bay (MEL). Fremantle, *W. H. Harvey*, Algae Australicae Exsiccatae 573, sub. *C. tomentosum* (BM, K, PC); ibid. Rottnest I. (TCD). Point Peron, 28.i.1950, *Royce* 513 (PERTH); 15.viii.1950, *Cribb* 69·27 (UC). Hamelin Bay, 21.x.1949, *Royce* 437 (PERTH). SOUTH AUSTRALIA: Marino, drift, 21.v.1953, *Womersley* (AD, A18,659) (UC). Elliston, upper sublittoral, 15.i.1951, *Womersley* (AD, A13,624) (UC). Coffin Bay, upper sublittoral, 10.i.1951, *Womersley* (AD, A13,775). Pig I., Pelican Lagoon, Kangaroo I., upper sublittoral, 2.xi.1947, *Womersley* (AD, A6157) (L, MICH, UC). Nora Creina, upper sublittoral pool, 14.xi.1955, *Womersley* (AD, A20,018). VICTORIA: Port Phillip, *Rawlinson* (TCD). Port Phillip Heads, 13.i.1891, *J. B. Wilson* (K); 1859, *F. von Mueller* (BM). Western Port, *F. von Mueller* (S). TASMANIA: Currie River, *Perrin & Lucas*, Mar. 1935 (CANB).

C. duthieae in Australia occurs mainly in relatively calm bays and inlets, from just below low tide level downwards.

This species has sometimes been referred in Australia to *C. elongatum* C. Agardh, a nomenclatural synonym of *C. decorticatum* (Woodw.) Howe, which is a closely related species from warm Atlantic waters (Harvey 1863, p. lvii; Sonder 1880, p. 38; Wilson 1892, p. 187; Lucas 1912, p. 171, pro parte). Specimens from Fremantle, with terete rather than complanate branches, were distributed (along with representatives of several other species) by Harvey as Algae Australicae Exsiccatae 573 (BM, K, PC, TCD) under the name *C. tomentosum* Stackhouse, an unrelated species restricted to the eastern North Atlantic.

11. **Codium harveyi** Silva, sp. nov.

Fig. 11; Plate 2, Fig. 1

Thallus erectus, ad 30 cm alt., (ad 10 ordines) dichotome ramosus; rami teretes, 5 mm dia. ad basim, ad 1 mm dia. prope apices attenuati. Utriculi pyriformes, 170–590 μ dia., 340–850 μ long., 1·3–2·5 plo longiores quam lati, apicibus late rotundatis; membrana utricularis 1·5 μ crass., prope apicem paululum ad modice (ad 24 μ) incrassata. Pili (aut pilorum cicatrices) multi in zona 135–240 μ infra apicem. Filamenta medullaria plerumque 34–62 μ dia., obturaculo sito juxta locum originis ex utriculo. Gametangia ovata ad lanceo-ovata, 68–136 μ dia., 150–240 μ long., 1–4 per utriculum, omnia in pediculis brevibus (c. 7 μ long.) in protuberantia in parte infima utriculi (310–480 μ infra apicem) portata.

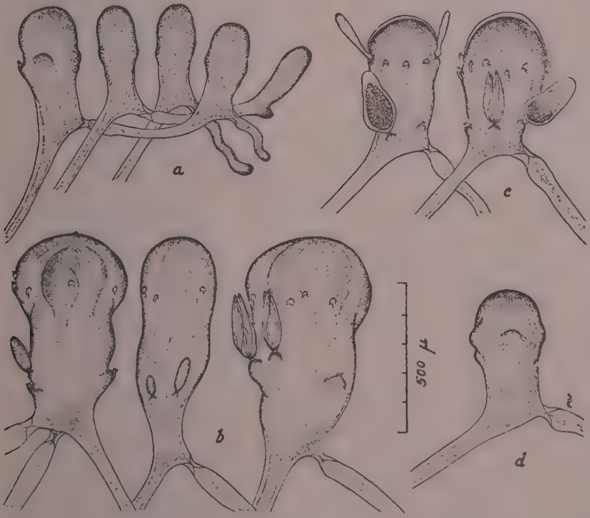

Fig. 11.—*C. harveyi*. *a*, *b*, Low Head, Tas., *Perrin*. *a*, utricles from tip; *b*, utricles from middle of frond; *c*, (Mouth of Tamar River, Tas., *Herb. Mackay*, K) utricles from middle of frond; *d*, (Long Bay, PortArthur, Tas., *Cribb* 65·3) utricle from middle of frond.

Thallus erect, to 30 cm high, dichotomously branched (to 10 orders); branches terete, 5 mm dia. at base, tapering to 1 mm dia. at apices. Utricles pyriform, 170–590 μ dia., 340–850 μ long, 1·3–2·5 × long as broad, with broadly rounded apices; utricular wall 1·5 μ thick, at apex slightly to moderately thickened (to 24 μ). Hairs (or hair scars) frequent, in zone 135–240 μ below apex. Medullary filaments mostly 34–62 μ dia., with plug close to point of departure from utricle. Gametangia ovoid to lance-ovoid, 68–136 μ dia., 150–240 μ long, 1–4 per utricle, each borne on short pedicel (about 7 μ long) on protuberance on lowermost part of utricle (310–480 μ below apex).

Type.—Vivonne Bay, Kangaroo I., S.A., 2.i.1949, drift, *Womersley* (AD, A10, 557). Isotypes in BM, UC.

Known Range.—Champion Bay, W.A., around southern Australia to Lake Macquarie, N.S.W.; Tasmania. New Zealand.

Representative Specimens Examined.—WESTERN AUSTRALIA: Champion Bay (MEL). SOUTH AUSTRALIA: Vivonne Bay, Kangaroo I., drift, 17.i.1950, *Womersley* (AD, A20,382). Lacepede Bay, 1895, *Englehardt* (BM, M). Nora Creina, 15 miles S. of Robe, 14.iii.1955, drift, *Womersley* (AD, A19,873). VICTORIA: Portland, drift, 7.i.1951, *C. Beauglehole* (AD, A15,650). Port Phillip Heads, 19.i.1886, *J. B. Wilson* (K). Phillip I., *F. von Mueller* (MEL). Portsea, Jan. 1919, *A. H. S. Lucas* (UC). TASMANIA: Low Head, Sept. 1950, *Mrs. F. Perrin* (UC). Long Bay, Port Arthur, 22.vi.1950, dredged, *Cribb* 65·3 (AD, F. MEL, UC). NEW SOUTH WALES: Eden, Jan. 1910, *A. H. S. Lucas* (UC). Jervis Bay, July 1899, cast up, *A. H. S. Lucas* (NSW). Lake Macquarie, *F. von Mueller* (M).

C. harveyi appears to be a sublittoral species of moderate to rough coasts.

C. harveyi and *C. australicum* Silva, sp. nov., heretofore have been confused with *C. muelleri*, which has thus gained an undeserved reputation for troublesome variability.

Although typical *C. harveyi* has been found on the east coast of Australia only as far north as Lake Macquarie, N.S.W., the influence of genes in this species may be seen in a population of intergrades extending to Rockingham Bay, Qld. (to be discussed under *C. australicum*).

A typical specimen collected in New Zealand by Dr. Lyall has been examined (BM).

12. **Codium muelleri** Kuetzing, Tab. Phyc. **6**: 34, pl. 95, **II** (1856). Sonder, Fragm. Phytogr. Aust. **11** (suppl.) p. 38 (Lefebre Peninsula specimen only) (1880). J. Agardh, Acta Univ. Lund. **23**: 42 (1887) (Fremantle specimen only). De Toni, Syll. Alg. **1**: 493 (1889) (Fremantle specimen only). Lucas, Proc. Linn. Soc. N.S.W. **37**: 171 (1912) (pro parte). Schmidt, Bibl. Bot., Stuttgart **23** (Heft 91): 51 (1923) (pro parte, et excl. fig. 35). Lucas, Seaweeds S. Aust. **1**: 54 (1936) (pro parte). Setchell, Proc. Nat. Acad. Sci., Wash. **26**: 444 (1940). Womersley, Trans. Roy. Soc. S. Aust. **73**: 145 (1950). Silva, Univ. Calif. Publ. Bot. **25**: 91, 92, 94, fig. 10 (1951). Womersley, Rep. Aust. Geogr. Soc. No. **1** (3B): 36 (1953).

Fig. 12

Codium schmidtii Vouk, Acta Bot., Zagreb **10**: 9, pl. 1, text-figs. 1–4 (1935).

Thallus erect, to 25 cm high, dichotomously branched (to 10 orders), branches terete, 5 mm dia. at base, 2·5–3 mm dia. above base, attenuating to 1·5 mm dia. at apices. Utricles irregularly cylindrical to pyriform, broadest about one-third below apex, 130–520 μ dia., 290–860 μ long, 1·5–3·5 × long as broad; apices truncate or broadly rounded; utricular wall 1·5 μ thick, at apex thin or occasionally thickened (to 54 μ), with an introrse umbo to 42 μ long. Hairs (or hair scars) common, one to several per utricle in zone 100–185 μ below apex. Medullary filaments mostly 28–62 μ dia., plug on outgoing side 80–350 μ from base of utricle. Gametangia ovoid, lance-ovoid, or ampulliform, 77–145 μ dia., 170–290 μ long, 1–4 per utricle, each borne on pedicel about 18 μ long on protuberance well below middle of utricle.

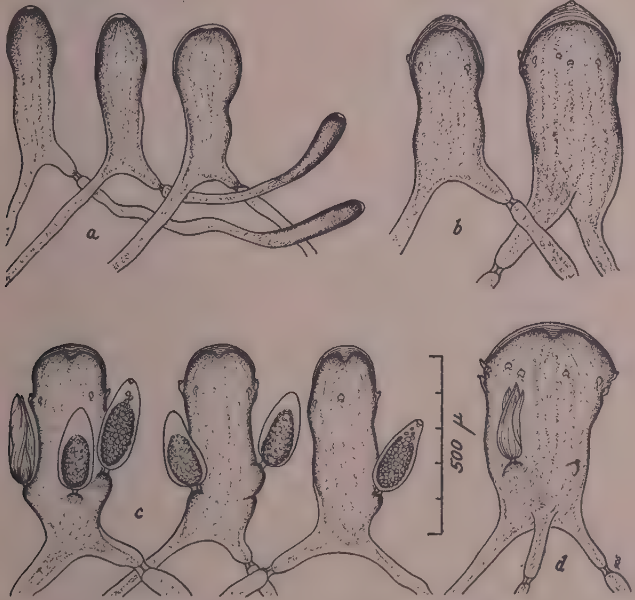

Fig. 12.—*C. muelleri*. *a*, *c*, *d*, Marino, Holdfast Bay, S.A., *Womersley* (AD, A18,661). *a*, utricles from tip; *b*, (Fremantle, W.A., *Royce* 1159) utricles from base; *c*, utricles from middle of frond; *d*, utricle from base.

Type.—Lefebre Peninsula, S.A., July 1852, *F. von Mueller* (L 937. 337–772).

Known Range.—Fremantle, W.A., around southern Australia to Rivoli Bay, S.A.

Representative Specimens Examined.—WESTERN AUSTRALIA: Rottnest I., 9.iv.1927, *W. A. Setchell* (UC). Fremantle, *W. H. Harvey*, Algae Australicae Exsiccatae 573 (LD, BM, K, NSW, US); drift, 10.iv.1952, *Royce* 1159, 1161 (PERTH, UC). Geographe Bay, 1879, *F. von Mueller* (MEL). King George's Sound, *W. H. Harvey*, Algae Australicae Exsiccatae 573, sub. *C. tomentosum* (BM). Israelite Bay, *Miss Brooks* (LD). SOUTH AUSTRALIA: Elliston, drift, 13.i.1951, *Womersley* (AD, A13,588). Marino, Holdfast Bay, drift, 21.v.1953, *Womersley* (AD, A18,661) (UC). Rocky Point Beach, Kangaroo I., drift, 4.vi.1947, *Womersley* (AD, A5715) (F). Kingscote, Kangaroo I., drift, 12.i.1948, *Womersley* (AD, A6957) (L). Lefebre Peninsula, July 1852, *F. von Mueller* (FI, L, MEL, PC). Cape Jaffa, drift, 31.viii.1949, Womersley (AD, A10,884) (MICH, UC). Rivoli Bay, *F. von Mueller* (MEL).

C. muelleri is a sublittoral species, found mainly in moderate to calm bays.

Setchell (1940) first showed that *C. schmidtii* is synonymous with *C. muelleri*.

Owing to the confusion of *C. harveyi* and *C. australicum* with *C. muelleri*, records of the latter species are especially unreliable and must be evaluated by examining the specimens upon which they are based. The following erroneous records of *C. muelleri* are based entirely on *C. harveyi* and *C. australicum*: Wilson 1892, p. 188; Lucas 1929*a*, p. 10; May 1938, p. 212; Guiler 1952, p. 75. The following records remain unverified: Levring 1946, p. 216; Lucas 1929*b*, p. 46; Reinbold 1899, p. 41. Along with other dichotomously branched species, *C. muelleri* has been erroneously referred to *C. tomentosum* (Sonder 1853, p. 660, pro parte; Harvey 1863, p. lvii, pro parte).

Although the easternmost record of unmistakable *C. muelleri* is Rivoli Bay, S.A., a specimen from Victoria (M) has been examined in which the utricles are similar to those of this species except that they are not regularly introrsely umbonate and the medullary filaments are plugged near their origin. The suggestion is that this specimen is a hybrid between *C. muelleri* and *C. harveyi*.

13. **Codium australicum** Silva, sp. nov.

Fig. 13; Plate 2, Fig. 2

Thallus erectus, ad 50 cm alt. (ad 20 ordines) dichotome ramosus; rami teretes, ad basim 5 (–10) mm dia., proxime super basim 3–6 mm dia., ad 2 mm dia. ad apices sensim attenuati. Utriculi cylindrici ad clavatos (100–) 130–210 (–300) μ dia., 460–800 μ long. (2–) 3–5 (–6) plo longiores quam lati, apicibus truncatis aut subrotundatis; membrana utricularis 1·5 μ crass., ad apicem plerumque paululum incrassata (–15 μ), interdum modice incrassata (–35 μ), apicibus incrassatis lamellatis, saepe interne alveolatis, interdum externe verruculosis, raro aliquantulum introrse umbonatis. Pili (aut pilorum cicatrices) frequentes, unus ad paucos per utriculum, in zona 65–130 μ infra apicem portati. Filamenta medullaria magna ex parte 20–35 μ dia., obturaculo plerumque 65–200 μ a basi utriculi sito. Gametangia anguste ellipsoideo-ovata aut cylindrica, 80–160 μ dia., 235–390 μ long., 1–3 per utriculum, omnia in pediculis *c.* 21 μ long., in protuberantia prope aut saepius infra partem mediam utriculi portata.

Thallus erect to 50 cm high, dichotomously branched (to 20 dichotomies), branches terete, 5 (–10) mm dia. at base, 3–6 mm dia. immediately above base, tapering gradually to 2 mm dia. at apices. Utricles cylindrical to clavate (100–) 130–210 (–300) μ dia., 460–800 μ long, (2–) 3–5 (–6) × long as broad, with truncate or slightly rounded apices; utricular wall 1·5 μ thick, at apex usually slightly thickened (–15 μ); at times moderately thickened (–35 μ), incrassate apices lamellate, often internally alveolate, sometimes externally verruculose, seldom slightly introrsely umbonate. Hairs (or hair scars) common, one to few per utricle, borne in zone 65–130 μ below apex. Medullary filaments mostly 20–35 μ dia., plug on outgoing side usually 65–200 μ from base of utricle. Gametangia narrowly ellipsoid-ovoid or cylindrical, 80–160 μ dia., 235–390 μ long, 1–3 per utricle, each borne on pedicel about 21 μ long on protuberance at or more often below middle of utricle.

Type.—Robe, S.A., 17.iii.1956, drift, *Elise Wollaston* (AD. A20, 409). Isotypes in BM, L, LD, MEL, NY, PC, UC.

Known Range.—Geographe Bay, W.A., around southern Australia to Tuggerah Lakes, N.S.W.; Tasmania. New Zealand.

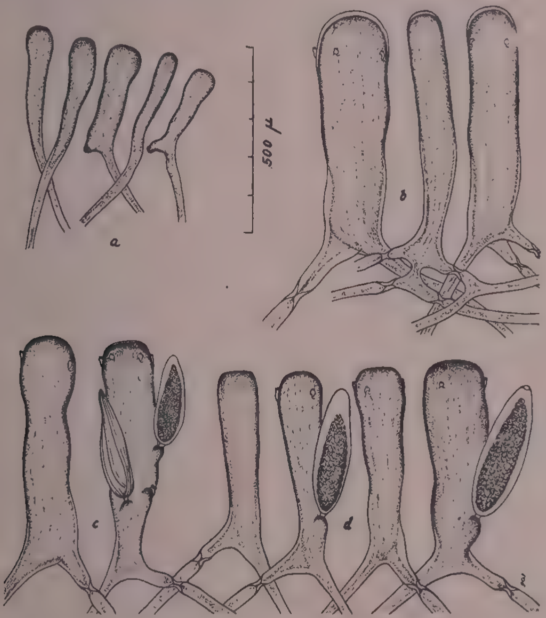

Fig. 13.—*C. australicum.* *a, b, d,* Port Arthur, Tas., *Cribb* 150·1. *a,* utricles from tip; *b,* utricles from base; *c,* (Marino, Holdfast Bay, S.A., *Womersley* (AD, A18,662)), utricles from middle of frond; *d,* utricles from middle of frond.

Representative Specimens Examined.—WESTERN AUSTRALIA: Geographe Bay, 1885, *Miss Priest* (MEL). King George's Sound, *W. H. Harvey* (TCD). SOUTH AUSTRALIA: Pondalowie Bay, drift, 24.iv.1955, *Womersley* (AD, A19,883). Marino, Holdfast Bay, drift, 21.v.1953, *Womersley* (AD, A18,662) (UC). Pennington Bay, Kangaroo I., drift, 27.i.1946, *Womersley* (AD, A2943). Robe, 17.iii.1956, drift, *Wollaston* (AD, A20,409). Nora Creina, 15 miles S. of Robe, 14.iii.1955, drift, *Womersley* (AD, A19,875). VICTORIA: Port Phillip Heads, 3.i.1890, *J. B. Wilson* (LD, BM). Woodbourne, Feb. 1949, *Iona Maclennan* (UC). Mouth of Hopkins River, *F. von Mueller* (MEL). NEW SOUTH WALES: Maroubra Bay, July 1910, *A. H. S. Lucas* (NSW). Entrance, Tuggerah Lakes, *Turner & Lucas* Dec. 1915 (CANB). TASMANIA: Marrawah, *Mrs. F. Perrin* (UC). Orford Beach, 20,vi.1950, drift, *Cribb* 64·1 (AD, MEL, UC). Port Arthur, 20.vi.1951, drift, *Cribb* 150·1 (UC 949, 773).

C. australicum is apparently (like *C. muelleri* and *C. harveyi*) a sublittoral species which rarely, if ever, reaches low tide mark. It occurs on moderate to rough coasts.

Two typical specimens purportedly from New Zealand have been examined: "New Zealand" (K); and "New Zealand, Antarctic Expedition 1839–1843, J. D. H[ooker]" (BM).

Although *C. australicum* and *C. harveyi* represent broad plateaus of morphological uniformity, the occurrence of a fairly large number of intergrades suggests hybridization between these two species. The following is a short series of intergrades running from *C. australicum* to *C. harveyi*: Oyster Bay, Tas. (NSW), typical *C. australicum* but with medullary filaments plugged near origin; Port Jackson, N.S.W., Feb. 1926, *A. H. S. Lucas* (UC), in which the presence of *C. harveyi* genes is manifested in the tendency toward pyriform utricles and medullary filaments with plugs fairly close to their origin; Port Phillip Heads, *F. von Mueller* (BM), similar to *C. harveyi* but with a tendency toward truncate apices.

C. australicum, *C. muelleri*, and *C. harveyi* comprise a closely related group of species. The first two share a character unique in the genus—the development of plugs in medullary filaments at a conspicuous distance from the base of the originating utricle. Evidence from putative hybridization points to a very close relationship between *C. australicum* and *C. harveyi*, but it should be remembered that degree of hybridization is not necessarily proportional to genotypic differences inasmuch as in the evolution of sympatric species divergence occurs only after the appearance of crossability barriers, which therefore are in effect selected.

14. **Codium fragile** (Sur.) Hariot, Mission scientifique du Cap Horn **5**: 32 (1889). Schmidt, Bibl. Bot., Stuttgart **23** (Heft. 91): 47 (1923). Lucas, Seaweeds, S. Aust., **1**: 54, fig. 37 (1936). May, Proc. Linn. Soc. N.S.W. **63**: 212 (1938). Levring, Acta Hort. Gothoburg. **16**: 216 (1946). Guiler, Pap. Roy. Soc. Tasm. **86**: 75 (1952).

Acanthocodium fragile Suringar, Ann. Mus. Bot. Lugduno-Batavi **3**: 258 (1867).

Codium mucronatum J. Agardh, Acta Univ. Lund. **23** (Afd. 3, Nr 2): 43, pl. I, figs. 2, 3 (1887). De Toni, Syll. Alg. **1**: 494 (1889). Wilson, Proc. Roy. Soc. Vict. **4**: 187 (1892). Lucas, Proc. Linn. Soc. N.S.W. **37**: 171 (1912). Cotton, Proc. R. Irish Acad. **31**:(15): 116 pl. 8, fig. 7 (1912). Lucas, Pap. Roy. Soc. Tasm. 1928: 10 (1929*a*).

Type.—Japan, *Textor* (L 910.187–1712).

Known Range.—Australia, New Zealand, Japan, Korea, China, Siberia; Alaska to Baja California, Mexico; southern Chile, Argentina, Falkland Islands; British Isles, Scandinavia, Netherlands, Atlantic and Mediterranean France, Meditteranean Spain; South West Africa around Cape of Good Hope to Robberg, Cape Province, South Africa.

C. fragile in southern Australia extends from the sublittoral zone into the lower littoral, on coasts of moderate to rough wave action. Often it is plentiful at low tide level.

The Australian representatives of this complex taxon were given taxonomic recognition by J. Agardh (as *C. mucronatum* var. *tasmanicum*). Although the morphological variation encountered among the Australian plants is so great that one might readily be led to question the usefulness or validity of recognizing infraspecific taxa, a careful study of a long series of collections (more than 200) has suggested that this species would best be treated as being represented by two subspecies in Australia with numerous intergrades.

14a. **Codium fragile** subsp. **tasmanicum** (J. Agardh) Silva, comb. nov.

Fig. 14*a*, *b*

Codium mucronatum J. Agardh var. *tasmanicum* J. Agardh, Acta Univ. Lund. **23** (Afd. 3, Nr. 2): 44, pl. 1, fig. 2 (1887). De Toni, Syll. Alg. **1**: 495 (1889); Lucas, Proc. Linn. Soc. N.S.W. **37**: 171 (1912).

Thallus comprising one to several erect, abundantly dichotomo-fastigiately branched fronds 10–30 cm high, attached to substratum by broad, spongy, basal disk; branches terete, 7–8 mm dia. at base, tapering to 3 mm at apices, dark green to blackish green, at times densely tomentose with long hyaline hairs. Young utricles slender, cylindrical; older utricles slightly clavate (70–) 130–330 (–390) μ dia. (710–) 1000–1450 (–1750) μ long (3–) 5–10 × long as broad; apices pointed; utricular wall 2 μ thick, thickened at apex and prolonging point into sharp mucro to 77 μ long. Hairs stout, gradually expanding upward, 52–104 μ dia. at apex; hair scars abundant in zone 185–450 μ below apex of utricle. Medullary filaments

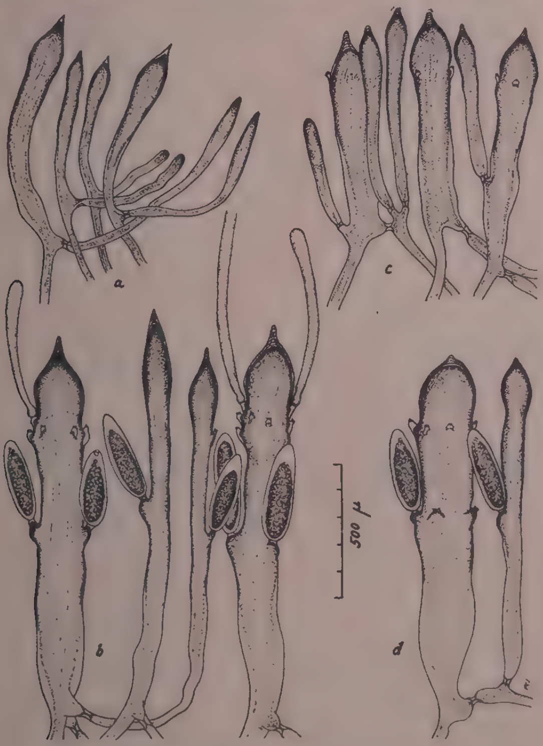

Fig. 14.—*a*, *b*, *C. fragile* subsp. *tasmanicum*. *a*, (Low Head, Tas., *Perrin*) utricles from tip; *b*, (Port Arthur, Tas., *Cribb* 126·9) utricles from middle of frond. *c*, *d*, *C. fragile* subsp. *novae-zelandiae*. *c*, (Narrabeen Head, N.S.W., *May* 2103) utricles from base; *d*, (Point Lonsdale, Vic., *Maclennan*) utricles from middle of frond.

mostly 26–46 μ dia. Gametangia lance-ovoid, narrowly ellipsoid, or cylindrical, 90–130 μ dia., 260–450 μ long, 1–4 per utricle, each borne on pedicel 10–14 μ long on protuberance 460–850 μ below apex.

Lectotype.—Tasmania, *R. Gunn* (LD, Herb. Agardh 15606).

Known Range.—Victor Harbour, S.A., to Walkerville, Vic.; Tasmania.

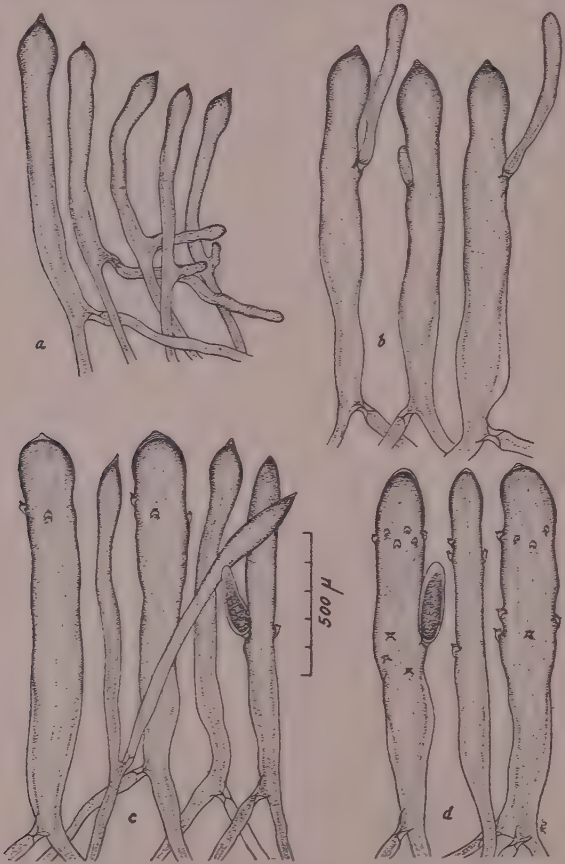

Fig. 15.—*C. fragile* subsp. *novae-zelandiae*: *a*, *b*, Robe, S.A., *Womersley* (AD, A10,998). *a*, utricles from tip; *b*, utricles from middle of frond; *c*, (New Zealand, *Berggren*=lectotype) utricles from middle of frond; *d*, (Port Phillip, Vic., L) utricles from middle of frond.

Representative Specimens Examined.—SOUTH AUSTRALIA: Victor Harbour, drift, 17.x.1948, *Womersley* (AD, A9291). VICTORIA: Port Fairy, *W. H. Harvey*, Algae Australicae Exsiccatae 573, sub. *C. tomentosum* (MEL). Port Phillip Heads, *J. B. Wilson*, 22.xi.1890 (K); 3.xii.1890 (MEL). Walkerville, lower littoral, Nov. 1949, *I. Bennett* (AD, A15,238). TASMANIA: *R. Gunn* (LD, K, MEL, S). Mouth of Tamar River, Jan. 1928, *A. H. S. Lucas* (UC). Georgetown, R. *Gunn*, Harvey's Algae Australicae Exsiccatae 573, sub. *C. tomentosum* (TCD). Low Head, Sept. 1950, *Mrs. F. Perrin* (UC). Port Arthur, 29.iii.1950, *Cribb* 48·8 (F, UC); 6.ii.1951, *Cribb* 126·9 (UC). Mouth of Currie River, 17.ix.1950, *Cribb* 75·1 (UC); 5.xii.1934, *L. M. Jones*, Tilden's South Pacific Plants, ser. 2, no. 209 (F).

14b. **Codium fragile** subsp. **novae-zelandiae** (J. Agardh) Silva, comb. nov.

Fig. 14*c*, *d*; 15

Codium mucronatum J. Agardh var. *novae-zelandiae* J. Agardh, Acta Univ. Lund. **23** (Afd. 3, Nr. 2): **44** (1887). De Toni Syll. Alg. **1**: 495 (1889).

Codium fragile (Sur.) Har. var. *novae-zelandiae* (J. Ag.) Collins, Tufts Coll. Stud. **3**: 99 (1912).

Differs from subsp. *tasmanicum* in that the apices of utricles tend to be rounded and bluntly mucronate.

Lectotype.—New Zealand, *S. Berggren* (LD, Herb. Agardh 15613).

Known Range.—Robe, S.A. to Ballina, N.S.W.; Tasmania. New Zealand. Argentina.

Representative Specimens Examined.—SOUTH AUSTRALIA: Robe, 29.viii.1949, *Womersley* (AD, A10,998) (L, MICH, S, UC). VICTORIA: Portland Bay, *F. von Mueller* (BM). Port Fairy, *W. H. Harvey*, Algae Australicae Exsiccatae 573, sub. *C. tomentosum* (BM). Port Phillip Heads, 22.xi.1890, *J. B. Wilson* (K). Brighton Beach, Port Phillip, 29.v.1948, *Womersley* (AD, A8329) (F). Point Lonsdale, Sept. 1948, *Iona Maclennan* (UC). NEW SOUTH WALES: Manly, near Sydney, 4.vi.1906, *Cheel* 20 (K). Narrabeen Head, near Sydney, 1.vii.1946, *May* 2103 (AHFH, UC). Ballina, *Henderson* (MEL). TASMANIA: Hunter Island, N.W. Tas., upper sublittoral, 14.i.1954, *I. Bennett* (AD, A19,668). Triabunna, 18.iii.1950, *Cribb* 41·9 (UC). Port Arthur, 22.i.1951, *Cribb* 115·13 (UC); River Derwent (K).

Although the Australian representatives of *C. fragile* may be arranged in a long series showing morphological intergradation, the distinctness of the extremes together with considerable geographic correlation makes the recognition of two subspecies feasible. The acuminate, sharply mucronate utricles typical of subsp. *tasmanicum* are to be found in most Tasmanian plants and in a few from Victoria and South Australia. The rounded and bluntly mucronate apices of utricles typical of subsp. *novae-zelandiae* are to be found in most plants from the Australian mainland. Intergrades (specimens which can be assigned to one or another subspecies only arbitrarily) are fairly common, though not abundant enough to make the recognition of subspecies impracticable.

Intergrades Examined.—WESTERN AUSTRALIA: Mabel Cove, west end of Rottnest I., 18.x.1934, *L. M. Jones*, Tilden's South Pacific Plants, ser. 2, no. 77 (F). VICTORIA: Port Fairy, *W. H. Harvey*, Algae Australicae Exsiccatae 573, sub. *C. tomentosum* (F). NEW SOUTH WALES: Eden, Jan. 1910, *A. H. S. Lucas* (UC). Long Bay, June 1898, *A. H. S. Lucas* (NSW).

A specimen of typical subsp. *tasmanicum* labelled Cape York (Queensland) has been found in the British Museum, but the locality is certainly questionable.

Plants of *C. fragile* were often reported as *C. tomentosum* Stackhouse in older literature (Hooker and Harvey 1847, p. 416; Harvey, 1860, p. 339; Harvey 1863, p. lvii, pro parte; Sonder 1880, p. 38, pro parte).

15. **Codium spinescens** sp. nov.

Fig. 16; Plate 3

Thallus dichotomus regulariter, ad 20 cm (aut plus) alt., rami teretes, tenues, 3 mm dia. ad basem, ad 1–2 mm dia. prope apices attenuati, virides aut fusco-virides. Utriculi juvenales tenues, utriculi ceteri crassi, irregulariter cylindrici ad clavatos, 80–270 μ dia., 475–680 μ long., 3–6 plo longiores quam lati; apices acuminati asymmetricaliter; membrana utricularis 2 μ crass., ad apicem incrassata cum longo prominenti mucrone; mucro cum tenuibus lamellis, saepe scalariformis (cum cubiculis) ad 80 μ long. Pili (aut pilorum cicatrices) frequentes, 4–8 per utriculum, positi in attenuata utriculi regione (170–240 μ infra apicem). Filamenta medullaria plerumque 20–30 μ dia. Gametangia ovata, ellipsoidea aut cylindrica, 70–160 μ dia., 175–240 μ long., 1–3 per utriculum, omnia in pediculis brevissimis in protuberantia infra partem mediam utriculi portata.

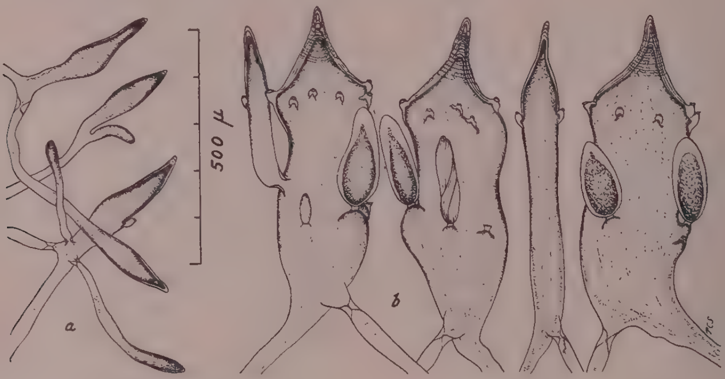

Fig. 16.—*C. spinescens.* Torpedo Rocks, Yallingup, W.A., *Royce* 616. *a*, utricles from tip; *b*, utricles from middle of frond.

Thallus regularly dichotomous, to 20 cm (or more) high; branches terete, slender, 3 mm dia. at base, tapering to 1–2 mm dia. at apices, medium to dark green. Young utricles slender, other utricles stout, irregularly cylindrical to clavate, 80–270 μ dia., 475–680 μ long, 3–6 × long as broad; apices asymmetrically acuminate; utricular wall 2 μ thick, at apex thickened and prolonging point into pronounced mucro; mucro finely lamellate, often scalariform (chambered), to 80 μ long. Hairs (or hair scars) common, 4–8 per utricle, borne in region where utricle begins to taper (170–240 μ below apex). Medullary filaments mostly 20–30 μ dia. Gametangia ovoid, ellipsoid, or cylindrical, 70–160 μ dia., 175–240 μ long, 1–3 per utricle, each borne on very short pedicel on protuberance below middle of utricle.

Type.—Ten miles east of Eucla (on S.A.–W.A. border), 3.ii.1954, drift, *Womersley* (AD, A19,240). Isotype in UC.

Other Specimens Examined.—WESTERN AUSTRALIA: Houtman Abrolhas (BM). Israelite Bay, Algae Muellerianae (MEL). Torpedo Rocks, Yallingup, W.A., 1.vi.1950, drift, *Royce* 616 (PERTH).

C. spinescens is closely related to *C. fragile*, from which it is readily distinguishable, however, by its very slender branches and short, stout, spinous utricles. Although morphologically it is, perhaps, no more different from certain segments of the *C. fragile* complex than forms that have been recognized by Silva as subspecies of *C. fragile* (for example, subsp. *scandinavicum* Silva 1957), its treatment as a species is probably justified in consideration of its geographical and morphological homogeneity and lack of intergradation.

Excluded Species.—The phycological literature pertinent to Australia contains many references to the first-described species of *Codium*, namely, *C. adhaerens* C. Ag., *C. bursa* (L.) C. Ag., *C. decorticatum* (Woodw.) Howe (or its nomenclatural synonym *C. elongatum* C. Ag.), and *C. tomentosum* Stackh. Careful study of these species shows that they are restricted to the Atlantic Ocean. In general, the applanate species have passed as *C. adhaerens*, the subglobose species as *C. bursa*, and the dichotomously branched species as *C. tomentosum*. *C. duthieae*, as previously indicated, was sometimes referred to *C. elongatum*. References to *C. decorticatum* from New South Wales and Queensland are to an undescribed species. It is regrettable that even in current literature (such as Guiler 1952) one may find references to European species that specialists long since have excluded from the Australian flora.

Phytogeographic Relationships.—Of the 15 species of *Codium* found in southern Australian waters, eight, constituting the largest geographical group, are endemic. With reference to their distribution, they may be listed as follows, from west to east: *C. laminarioides*, *C. spinescens*, *C. muelleri*, *C. harveyi*, *C. australicum*, *C. pomoides*, *C. capitulatum*, *C. perrinae*. The next largest group comprises those species which also occur in South Africa: *C. duthieae*, very likely *C. lucasii*, and possibly *C. galeatum*. Two species, *C. mamillosum* and *C. spongiosum*, are Indo-Pacific in affinity; of these, *C. spongiosum* also occurs in South Africa. Finally, *C. fragile* and *C. dimorphum* are antarctic circumpolar in distribution, the former being pantemperate and bipolar in addition.

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The authors are indebted to the directors and curators of the various herbaria listed in the Introduction for making specimens available for study.

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THE GENUS CODIUM IN SOUTHERN AUSTRALIA

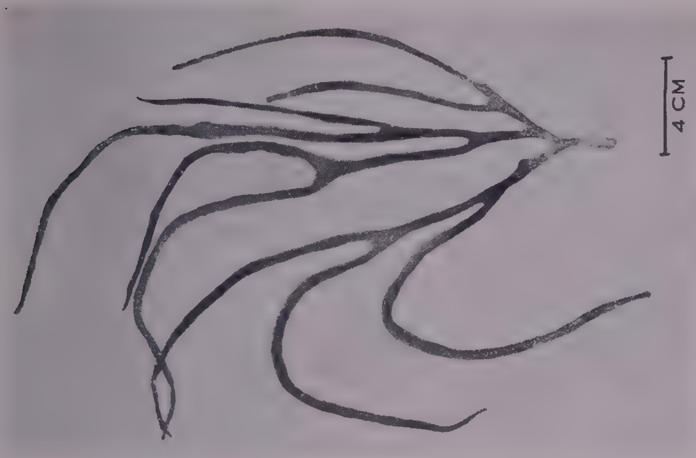


Fig. 2.—*C. duthieae.* Elliston, S.A., Womersley (AD, A19,385).

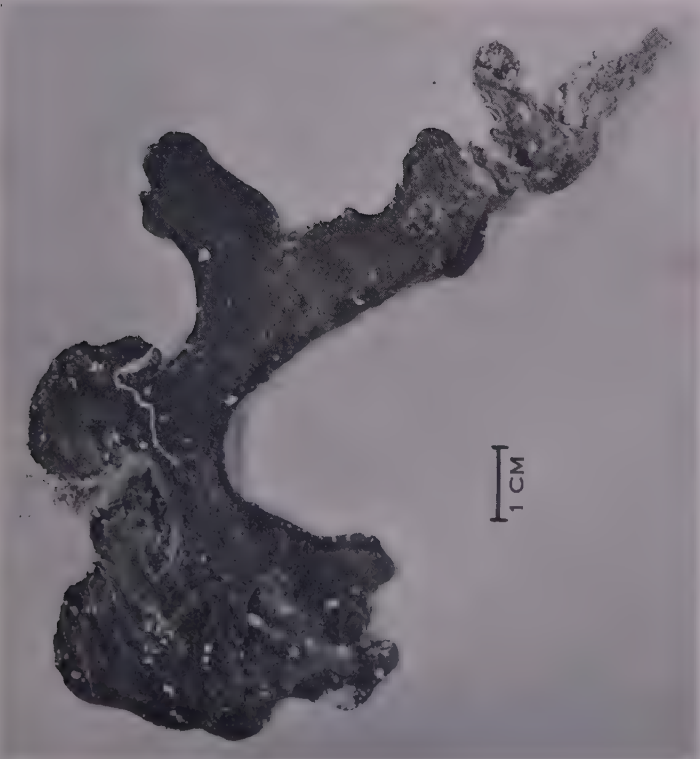


Fig. 1.—*C. capitulatum.* Elliston, S.A., Womersley (AD, A19,384, type).

THE GENUS CODIUM IN SOUTHERN AUSTRALIA

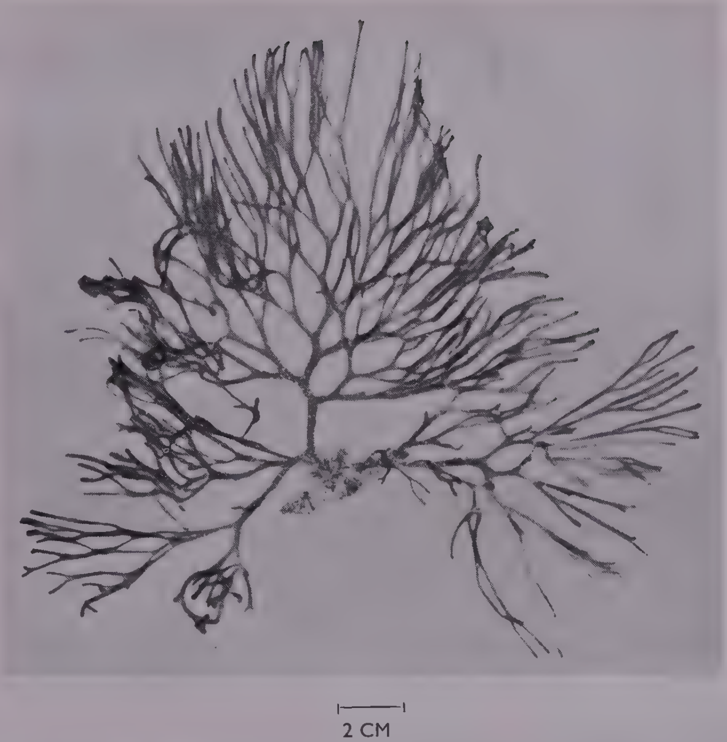


Fig. 1.—*C. harveyi*. Vivonne Bay, Kangaroo I., S.A., *Womersley*
(AD, A10,557, type).

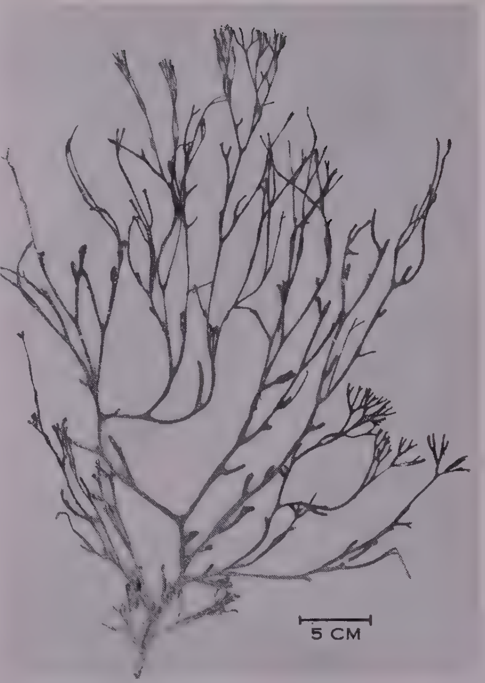
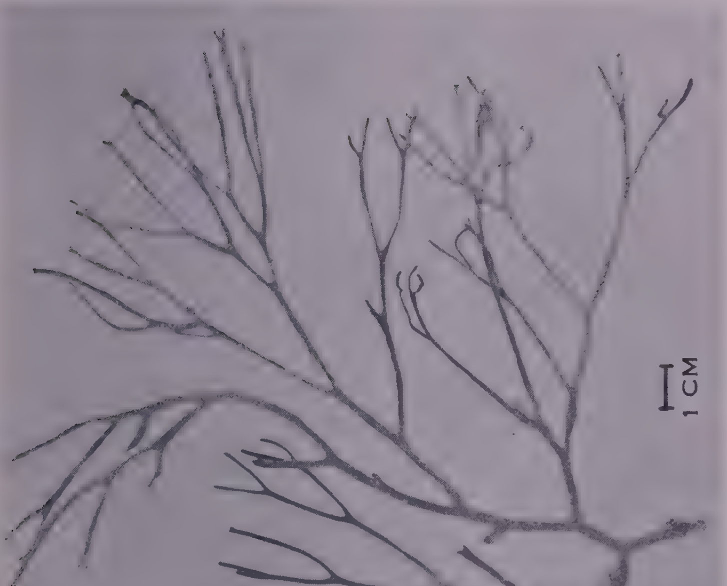


Fig. 2.—*C. australicum*. Robe, S.A., Wollaston.
(AD, A20,409, type).

THE GENUS CODIUM IN SOUTHERN AUSTRALIA



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